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Zoogeographical Regionalization of the World Based on the Distribution of the Members of the Order *Carnivora (Mammalia)*

[Pp. 309—396, 63 text-figures]

Zoogeograficzna regionalizacja świata na podstawie rozmieszczenia przedstawicieli rzędu *Carnivora (Mammalia)*

Зоогеографическая регионализация мира на основании географического распространения представителей отряда хищных млекопитающих *(Carnivora, Mammalia)*

Abstract. The paper presents an analysis of the occurrence of the *Carnivora (Mammalia)* throughout the world. It has permitted the characterisation of the fauna of this group in particular zoogeographical provinces and the definition of their boundaries. The distribution of particular carnivore families has also been discussed.

CONTENTS

I. INTRODUCTION

The zoogeographical regionalization of the world is a very complex problem, with a long history. Many zoologists made attempts to divide the world into zoogeographical regions, in which they based themselves chiefly on the distribution of vertebrates, above all, that of mammals and birds (SCLATER, 1858; WALLACE, 1876; LYDEKKER, 1896, and others).

SCLATER (1858) distinguished six fundamental zoogeographical regions of the world: the Palaearctic, Nearctic, Oriental, Ethiopian, Neotropical and Australian. His division has been maintained up to now only that some zoogeographers combine the Palaearctic and Nearctic into one region, the Holarctic (the name suggested by HEILPRIN in 1867). In this paper I use the name Holarctic, because quite a number of facts which indicate a close relationship between these regions justify their union. I shall still return to this subject in another place of this paper.

The zoogeographical division of particular regions into provinces and areas and sometimes also the course of the boundaries between them are controversial. A number of such attempts at regionalization have been made since the times of WALLACE. They aimed at the elaboration of a general zoogeographical division of the world which would fully satisfy the zoologists concerned with the distribution of various groups of animals. Nevertheless, in view of the vast diversity of the animal kingdom and the existence of different factors which do not allow the reduction of the zoogeographical regionalization of the world to a common denominator, each succeeding study in this field is at the most only an approach to the generalization or a trial of it but in no case a definite solution.

For this very reason the present paper does not claim the attainment of the decisive universal regionalization either, which besides is not attainable at all, but is only an attempt to apply the statistical methods used recently by KOSTROWICKI (1965, 1969) and JACZEWSKI and KOSTROWICKI (MS.) in the zoogeography of insects for the zoogeography based on one mammalian order, the *Carnivora*.

In the paper I adopted the division into regions, provinces and areas, assuming the full equivalence of particular units of the same level of division. It is obvious that no comparisons would have been possible without such an assumption.

As regards the nomenclature used, I, as a rule, based the division into zoogeographical regions on that adopted in the Atlas of Physical Geography of the World published by the U. S. S. R. Academy of Sciences in 1964. Examples of various types of zoogeographical regionalization were given by KOSTROWICKI (1965) in his publication on the regionalization of the *Macrolepidoptera* of the Palaearctic.

Working at the zoogeography of mammals, I reflected on the choice of an order which would be the most suitable for its purposes. It would have to

fulfil the following conditions: it ought to be widely distributed all over the globe, to contain a relatively great number of well-differentiated species allowing the application of statistical analyses, and to be relatively well known in so far as the ranges of occurrence of particular species are concerned.

The order *Carnivora*, suggested by Prof. T. Jaczewski, satisfies these conditions thoroughly: it numbers 247 species, which are more or less uniformly distributed in various continents (except Australia) and being sufficiently well known themselves have ranges fairly closely examined. The systematic position of most of these species is well known except for some controversial species only, which will be discussed in Section III.

I thought over the possibility of inclusion of subspecies in the statistical analysis but this had to be given up, because the subspecific taxonomy of most carnivore species, as well as that in other mammalian orders, is now so obscure that it would practically make all the comparison impossible. This is why I confined myself only to species, and the result of my study has confirmed my assumptions about the sufficient amount of comparative material.

I wish to express my thanks to Prof. J. Wengris for valuable remarks which she lavished on me during my work, to Prof. T. Jaczewski and Dr. A. S. Kostrowicki for their help and advice concerning the elaboration of material and to Dr. R. Kraft and Dr. Cz. Platt for their assisting me in statistical elaboration of the results.

II. MATERIAL AND METHOD

The choice of the order *Carnivora* as the subject for this study has been justified in the Introduction. Most carnivores are flesh-eating animals; they generally live on plant-eating animals — rodents, ungulates, etc. — and, therefore, they have indirect connections with the nature of the environment in which they live. There is also a relationship between the nature of the plant cover of a given area and the fauna occurring there (forest, steppe, desert and other faunas). The foregoing statements were the starting point of further considerations.

I constructed a list of living carnivores on the basis of faunal specifications for various countries and geographical areas (see References and respective quotations in the discussion of particular regions).

I used the following criteria in constructing the list of species:

— I united the forms the taxonomic distinctness of which I considered to be dubious and as to which the data from literature show that we are concerned with one species, e. g., *Lynx lynx* (synonyms *Lynx pardalis* and *Lynx canadensis*);

— I rejected local „species", e. g., a few tens of „species" of the bear described by Merriam from North America (Hall and Kelson, 1959);

— I did not include the acclimatized forms, which would have confused the

picture, e. g., *Nyctereutes procyonoides* in Europe, *Herpestes javanicus* on the Antilles, etc.

Having made the list of species, I still had to prepare a list of working areal units so as to compare their carnivore faunas. I resolved to base these units on the geobotanical regions, on assumption that they cover areas of identical or very similar ecological conditions. Basing myself on the Atlas of Physical Geography of the World (1964), I chose 113 working areal units covering all the continents (Australia, having only one carnivore species, was treated as one unit). In the discussions of particular provinces (Section III) I give short geobotanical characteristics of these units, but naturally they are very general. Detailed descriptions may be found in appropriate publications on phytogeography. As to the geobotanical formations, I utilized the information obtained from the publication by Alekhin et al. (1961).

The serial numbers with which all working areal units are provided correspond to those used on the maps and in the diagrams.

As a result of the statistical analysis, a number of the units have been united on account of the close relationship of the carnivore faunas inhabiting them.

List of Working Areal Units

1. Mediterranean formations of Africa
2. Sahara
3. Southern Sahara—Nubia
4. Savannas of Central Africa
5. Zone of African parkland
6. Zone of African tropical rain forests
7. Tropical rain forest of the Congo
8. Dry forests of Angola
9. Savannas of South Africa
10. Deserts and semi-deserts of South Africa
11. Semi-deserts of South-Western Africa
12. Cape Province
13. Transvaal savannas
14. Dry forests of Rhodesia
15. Savannas of East Africa
16. Dry Somalian and Ethiopian forests
17. Somalian deserts
18. Dry forests of Madagascar
19. Savannas of Central Madagascar
20. Damp forests of Madagascar
21. Western part of Mediterranean formations of Europe
22. Mediterranean Islands
23. Iberian Peninsula
24. Pyrenees
25. Apennine Peninsula
26. Alps
28. Western Atlantic formations
29. Scotland
30. Central Europe
31. Carpathians
32. North Europe
33. East European steppes
34. North European tundra
35. Scandinavian mountains
36. Black Sea steppes
37. Siberian tundra
38. West Siberian taiga
39. Transvolga-Kazakh steppes
40. Subarctic Siberian Uplands
41. East Siberian taiga
42. Kamchatka
43. Ussuriisk region and Sakhalin
44. Manchuria and North China
45. North Japan
46. Southern parts of China, Japan and Korea
47. Altai
48. Mongolian-Chinese steppes
49. Deserts of Central Asia
50. Mountains of South China
51. Turanian-Caspian deserts
52. Tibet
53. Tien Shan
54. Karakoram—Himalayas
55. Subtropical slopes of the Himalayas
56. Caucasus
57. Transcaucasian steppes

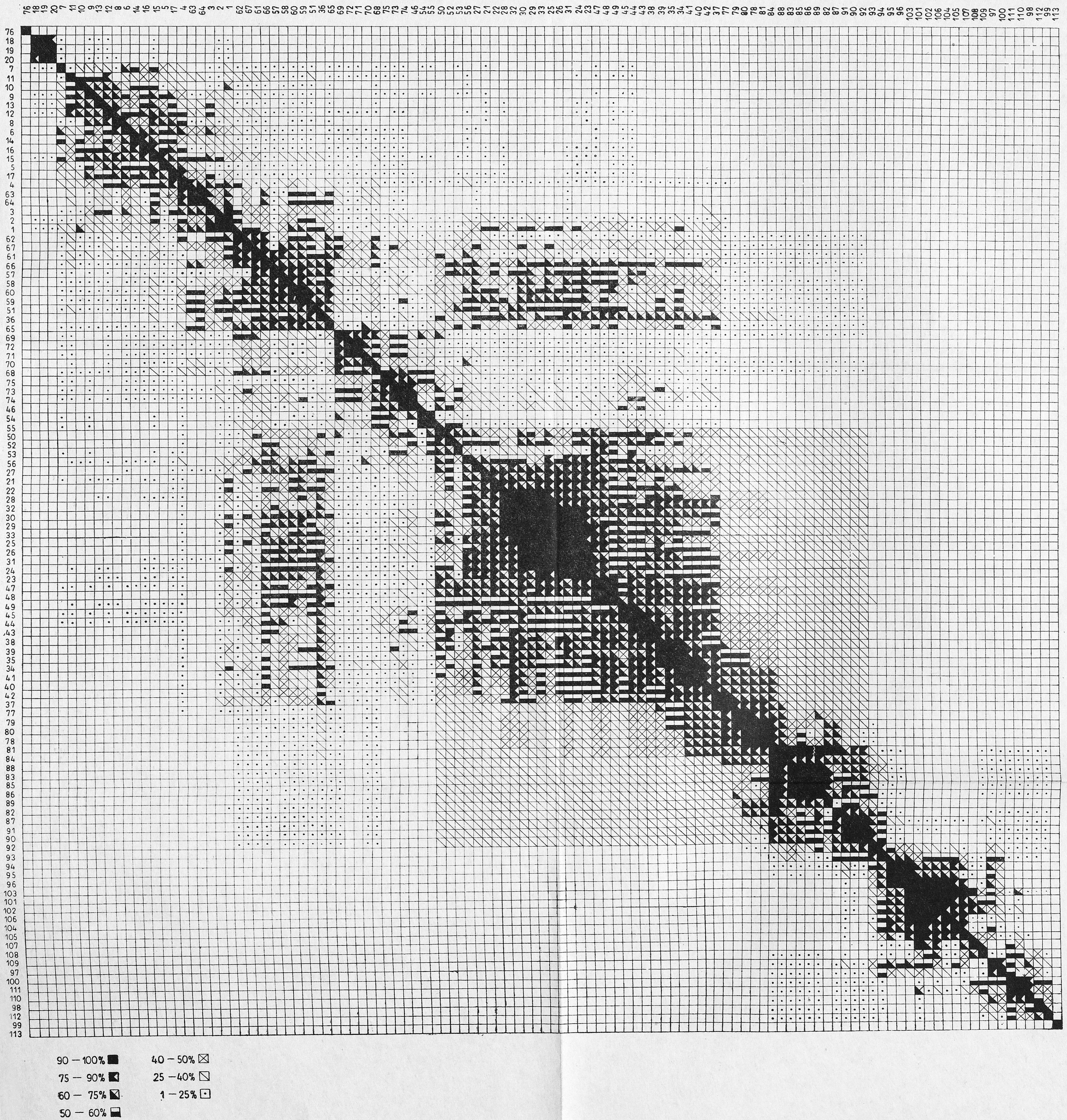


Fig. 1. CZEKANOWSKI'S diagram, showing the affinities of separate local faunas

58. Mesopotamia
59. Levant
60. Anatolia
61. Syrian deserts
62. Arabian deserts
63. Savannas of Southern Arabia
64. Yemen
65. Iran-Afghanian uplands
66. Deserts of Afghanistan and Pakistan
67. Savannas of Punjab
68. Forests of Central India
69. Jungles ot Bengal
70. Savannas of Dekan
71. Jungles of Ceylon
72. Dry forests of Ceylon
73. Upland jungles of Burma and Indo-China
74. Lowland jungles of Indo-China
75. Indonesia and Philippine Is.
76. Australia
77. American Arctic
78. Canadian taiga
79. Aleutian zone
80. Mountains of Alaska and Northern Canada
81. Taiga of Northern Rocky Mountains
82. Mixed forests of Canada
83. Mixed forests of U. S. A.
84. British Columbia
85. Great Prairies
86. West American uplands
87. California
88. Deserts of Colorado
89. Atlantic and Florida zone
90. Steppes of Mexico and Texas
91. Deserts of Arizona and Mexico
92. Uplands of Central America
93. Tropical forests of Mexico
94. Tropical forests of Central America
95. Orinoco Savannas
96. Forests of Guyana
97. Damp forests of Andes
98. Central Andes-Puna
99. Subantarctic Andes
100. Deserts on the Pacific Coast
101. Tropical forests in the basin of the Amazon
102. Savannas of Brazil and Bolivia
103. East Brazilian steppes
104. South Brazilian forests
105. East Brazilian forests
106. Gran Chaco
107. Subtropical forests of Brazil and Uruguay
108. Pampas
109. Subtropical formations of the Andes
110. Patagonian deserts
111. Patagonian „steppes"
112. Chilean forests
113. Antilles

As can be seen from the statistically elaborated material, this division is too detailed, especially as regards Europe and America, and for this reason a number of units have been combined. A full list of these new units will be given in the next section.

The list of carnivore species was used to construct collective charts, the occurrence or lack of a species in a given working areal unit being marked in appropriate columns. These charts provided a picture of local faunas, which have been worked out by the methods of differential analysis, the linear (CZEKANOWSKI'S diagram) and the dendritic (CZEKANOWSKI, 1913; PERKAL, 1958).

CZEKANOWSKI'S method, used mainly in anthropology and craniometry, has been applied in phytogeography, by KULCZYŃSKI (1940), and also in phytosociology. KOSTROWICKI (1965) introduced it into zoogeography. This method allows comparison of any number of elements in a highly objective manner.

Using it, we acquire, in the statisticians' opinion, a system of components examined, the characteristics of which become arranged according to their value. Its objectiveness consists in the fact that it cannot give two different results, the conclusions are easy to check (by other persons) and provide valuable

material for interpretation. The method is very laborious since it demands a great many calculations.

In this paper I adopted the index of faunal affinity after Kostrowicki. Here, the degree of affinity is expressed by Szymkiewicz's formula (Szafer, 1949),

$$p = \frac{a}{A} \times 100 \, ,$$

in which p is the index of affinity; a is the number of common species of the faunas A and B; A is the number of species of the poorer fauna (A).

This index expresses the affinity of the faunas being compared. Its disadvantage is the fact that it shows only the percentage share of the species of the more abundant fauna in the poorer one but not vice versa. However, according to Kostrowicki (1965), with whom I quite agree, in general regionalization these differences are not significant, because here we are concerned with the affinity of the faunas and not with the share of particular elements in them.

The indices of affinity calculated for all the working areal units have been set in order by Czekanowski's method and the dendritic method and are presented in the form of diagrams. The results obtained are plotted on the maps showing the zoogeographical regionalization of the world.

III. ANALYSIS OF RESULTS

The results of statistical analyses are presented in the diagrams. A comparison of the two methods used shows the full correspondence of the results expressed by them. The dendritic method was, however, only a secondary one and for this reason in the discussion of particular units of the zoogeographical division I based myself, above all, on Czekanowski's diagram. In the zoogeographical division of the world, presented below, the figures in brackets correspond to those of the working areal units plotted on the maps.

I. Holarctic Region

1. Arctic Province
   A. Eurasian Area (37)
   B. American Area (77)
2. Boreal Province
   A. Alasko-Canadian Area (78, 79, 80, 81)
   B. Europeo-Siberian Area (34, 35, 38, 40, 41)
   C. Kamchatka Area (42)
   D. Kazakh-Chinese Area (39, 43, 44, 45)
   E. Altai-Mongolian Area (47, 48, 49)
   F. European Area (23, 24, 25, 26, 28, 29, 30, 31, 32, 33)
3. Mediterranean Province
   A. Iberian Area (21)

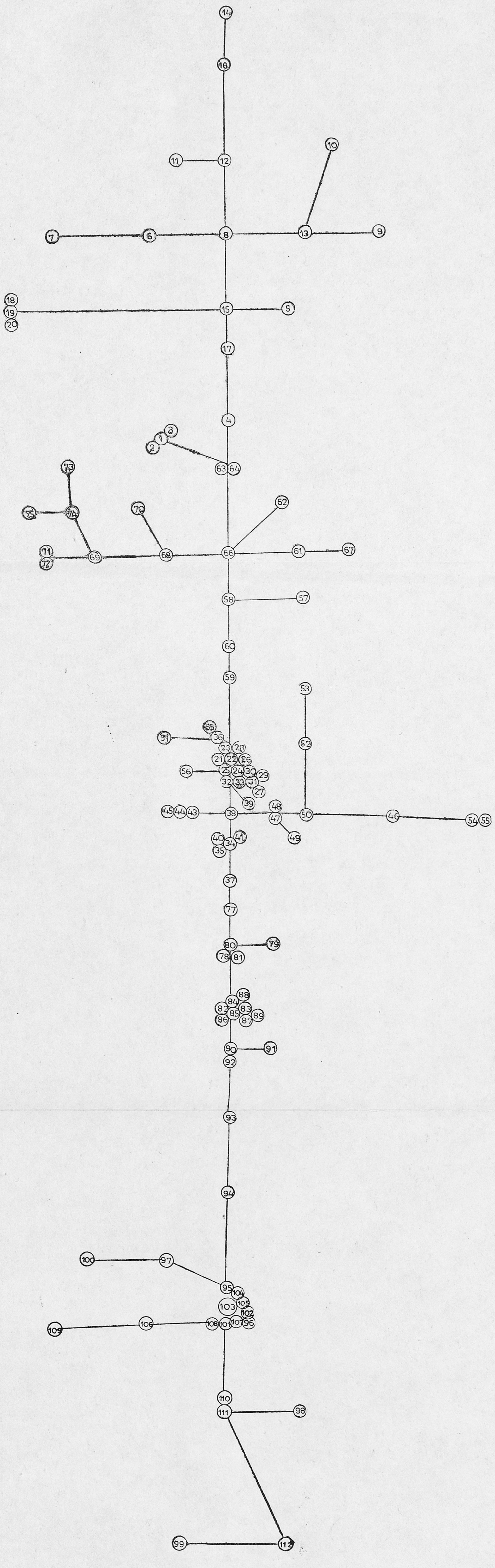


Fig. 2. A dendritic diagram, showing the affinities of separate local faunas

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B. Area of Mediterranean Islands (22)
C. Balkan Area (27)
D. Caucasian Area (56)
4. Central Asiatic Province
A. Tien Shan Area (53)
B. Tibet Area (52)
C. South Chinese Area (50)
5. Levanto-Turanian Province
A. Afghan Area (65)
B. Black Sea Area (36)
C. Turano-Caspian Area (51)
D. Levant Area (59, 60)
E. Iran Area (58)
F. Transcaucasian Area (57)
6. Arabo-Punjab Province
A. Arabian Area (62)
B. Punjab Area (67)
C. Syrian Area (61)
D. Pakistan Area (66)
7. American Province
A. Canadian Area (82)
B. American Temperate Area (83, 84, 85, 86, 88, 89)
C. Californian Area (87)
D. Sonoran Area (90, 91, 92)

II. Oriental Region

1. Sino-Malay Province
A. Himalayan Area (54, 55)
B. Chinese Area (46)
C. Indo-Chinese Area (74)
D. Burmo-Indo-Chinese Area (73)
E. Indonesian-Philippine Area (75)
2. Indian Province
A. Bengal Area (69)
B. Ceylon (71, 72)
C. Dekan Area (70)
D. Central Indian Area (68)

III. Australian Region (76)

IV. Ethiopian Region

1. Malagasy Province (18, 19, 20)
2. Congolese Province (7)
3. South African Province

A. South-Western Area (11)
B. Southern Desert Area (10)
C. South African Area (9)
D. Transvaal Area (13)
E. Cape Area (12)
F. Angolan Area (8)
G. Equatorial Area (6)

4. East African Province
A. Rhodesian Area (14)
B. Somalo-Ethiopian Area (16)
C. East African Area (15)
D. Nigerian Area (5)
E. Somalian Desert Area (17)
F. Central African Area (4)

5. North African-Yemen Province
A. North African Area (1, 2, 3)
B. Yemen Area (63, 64)

V. Neotropical Region

1. Guyano-Brazilian Province
A. Mexican Area (93)
B. Central American Area (94)
C. Amazon Area (95, 96, 101, 102, 103, 106)
D. Brazil-Uruguay Area (104, 105, 107, 108)

2. Andean Province
A. Subtropical Area (109)
B. Subandean Area (97)
C. Pacific Area (100)

3. Patagono-Andean Province
A. Argentine Area (110, 111)
B. Central Andean Area (98)
C. Chilean Area (112)
D. Subantarctic Area (99)

4. Antillean Province (113)

This list, presenting the regional division of the world based on the distribution of the contemporary members of the order *Carnivora*, departs in some points from the generally accepted zoogeographical divisions even at the highest level, i. e., that of regions (Fig. 3). An essential difference are the changes in the course of the boundary between the Holarctic and both the Ethiopian and Oriental Regions. These problems will be discussed in detail in appropriate parts of this paper, since they constitute a primary result of the statistical analyses. Here I should like to emphasize only that the zoogeographical regio-

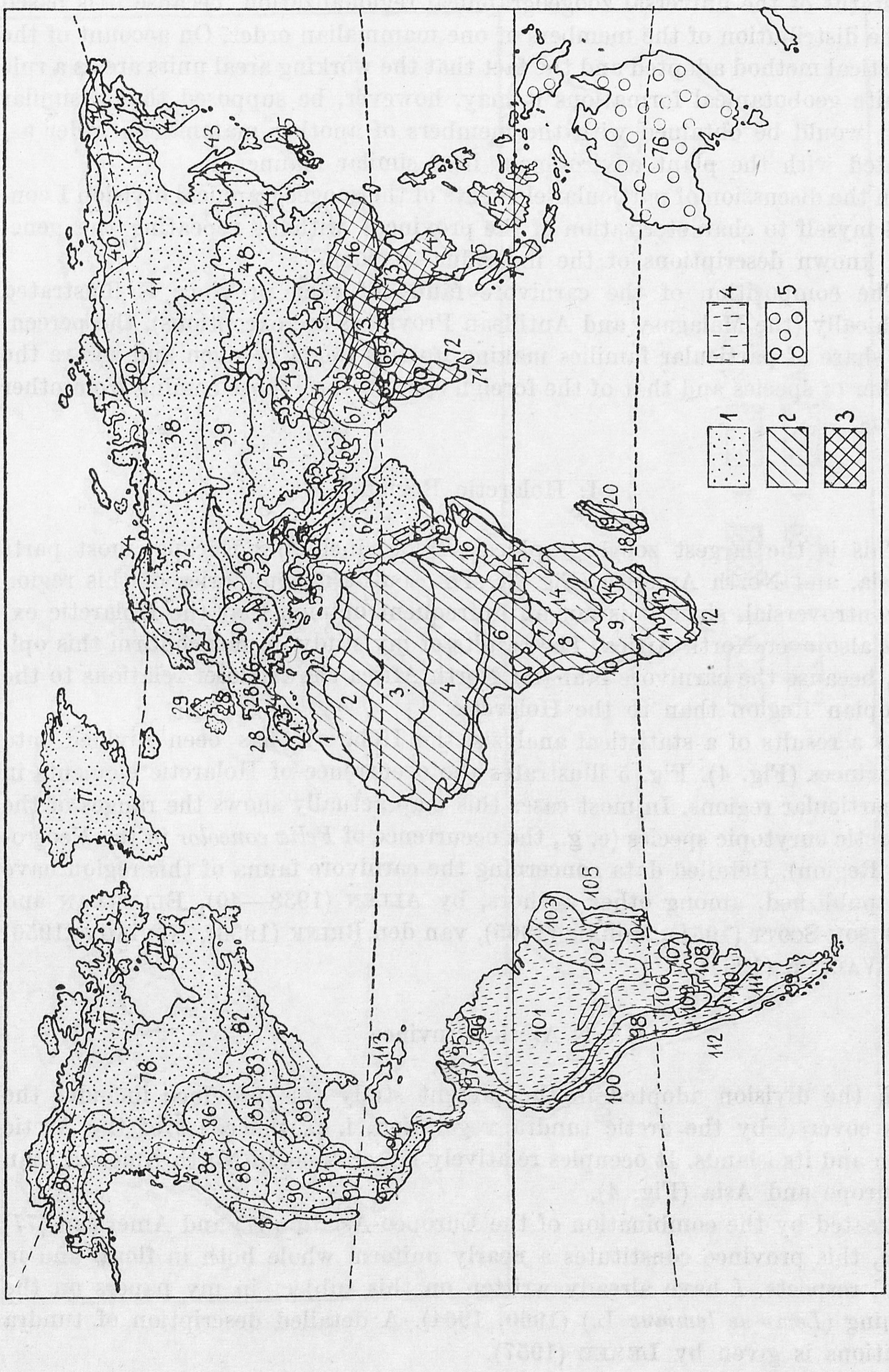


Fig. 3. A division of the world into zoogeographical regions. 1 — Holarctic Region, 2 — Ethiopian Region, 3 — Oriental Region, 4 — Neotropical Region, 5 — Australian Region

nalization of the world resulting from the present investigation does not claim the status of the universal zoogeographical regionalization, because it is based on the distribution of the members of one mammalian order. On account of the statistical method adopted and the fact that the working areal units are as a rule definite geobotanical formations it may, however, be supposed that a similar result would be obtained with the members of another mammalian order associated with the plant environment in a similar manner.

In the discussion of particular elements of the zoogeographical division I confined myself to characterization of the provinces without repeating the generally known descriptions of the individual regions.

The composition of the carnivore fauna of each province is illustrated graphically (the Malagasy and Antillean Provinces are exceptions), the percentage share of particular families making up this fauna is given and so are the number of species and that of the foreign species, i. e., those coming from other regions.

I. Holarctic Region

This is the largest zoogeographical region, including Europe, most parts of Asia, and North America (Fig. 3). The southern boundaries of this region are controversial, since it is not an unfrequent opinion that the Holarctic extends also over North Africa. The results of my study do not confirm this opinion, because the carnivore fauna of North Africa shows closer relations to the Ethiopian Region than to the Holarctic.

As a results of a statistical analysis, the Holarctic has been divided into 7 provinces (Fig. 4). Fig. 5 illustrates the occurrence of Holarctic elements in the particular regions. In most cases this map actually shows the ranges of the Holarctic eurytopic species (e. g., the occurrence of *Felix concolor* in the Neotropical Region). Detailed data concerning the carnivore fauna of this region have been published, among other authors, by Allen (1938—40), Ellerman and Morrison-Scott (1951), Morris (1965), van den Brink (1956), Novikov (1956) and Walker (1964).

1. Arctic Province

In the division adopted in the present study this province includes the areas covered by the arctic tundra vegetation, i. e., the coast of the Arctic Ocean and its islands. It occupies relatively larger areas in North America than in Europe and Asia (Fig. 4).

Created by the combination of the Europeo-Asiatic (37) and American (77) Areas, this province constitutes a nearly uniform whole both in floral and in faunal respects. I have already written on this subject in my papers on the lemming (*Lemmus lemmus* L.) (1960, 1964). A detailed description of tundra conditions is given by Lemee (1957).

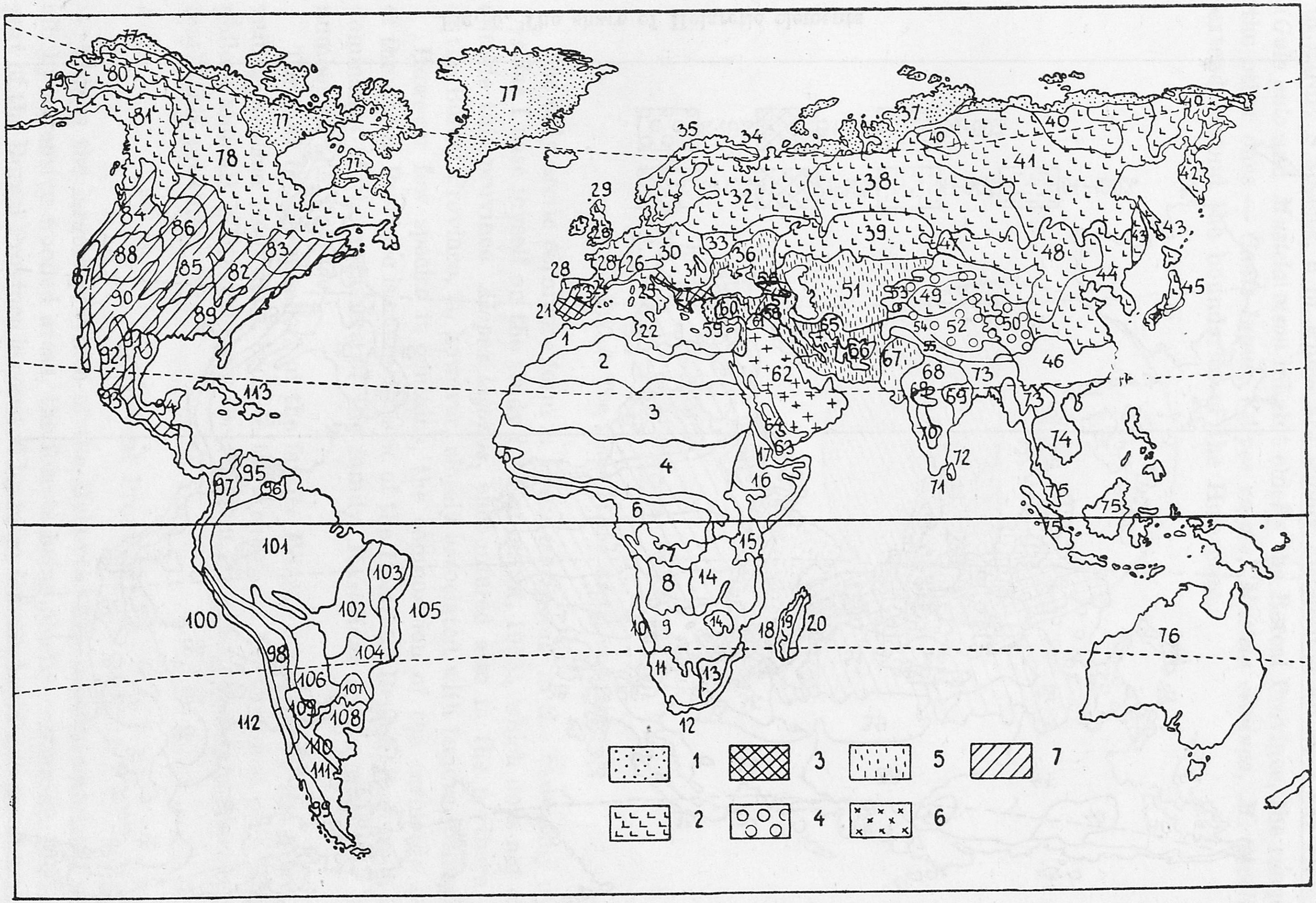


Fig. 4. Provinces of the Holarctic Region. 1 — Arctic, 2 — Boreal, 3 — Mediterranean, 4 — Central Asiatic, 5 — Levanto-Turanian, 6 — Arabo-Punjab, 7 — American

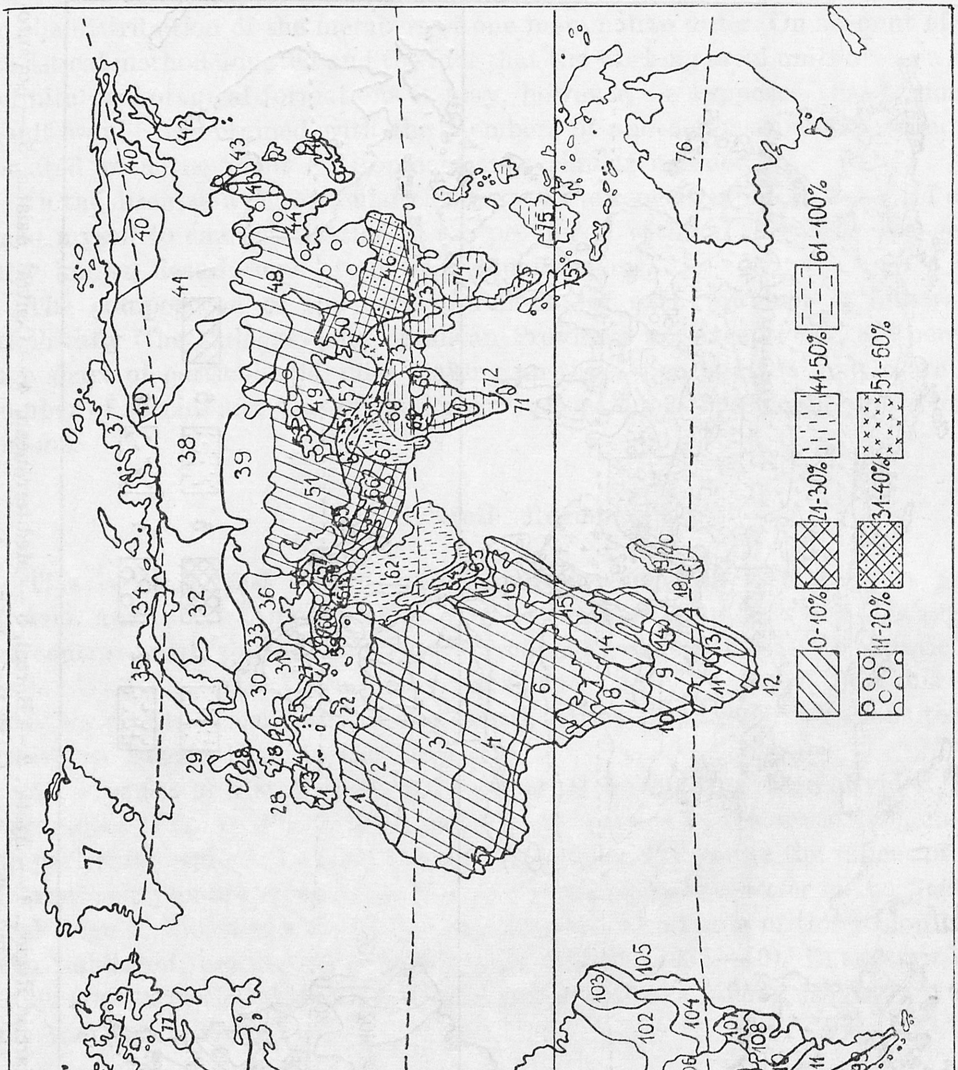


Fig. 5. The share of Holarctic elements

The carnivore fauna of the Arctic Province is poor (Fig. 6), as it consists of hardly 8 species, 6 of which are widely distributed all over the Holarctic (*Gulo gulo* and *Mustela vison* inhabit chiefly the Boreal Province, the ranges of the other ones — *Canis lupus*, *Vulpes vulpes*, *Mustela erminea*, *M. nivalis* — extend beyond the boundaries of the Holarctic).

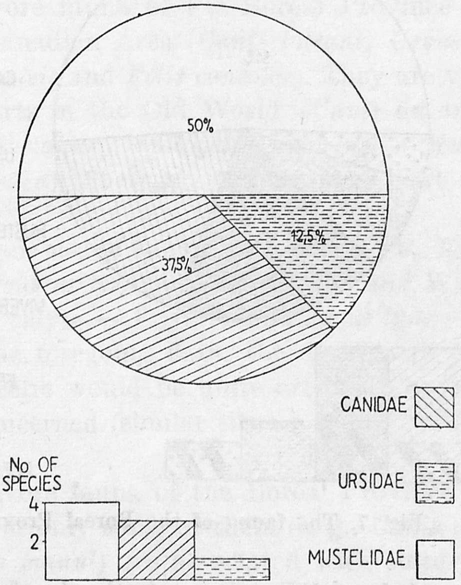


Fig. 6. The fauna of the Arctic Province

The only arctic cornivore form is *Ursus maritimus* (in the taxonomy of the *Ursidae* I base myself on the study by ERDBRINK, 1953), which does not occur outside this province. *Alopex lagopus*, encountered also in the northern part of the Boreal Province, is, however, closely associated with tundra formations.

However few species it contains, the composition of the carnivore fauna of the Arctic Province is characteristic of the Holarctic Region: it shows a clear dominance of the members of the family *Mustelidae* and a relatively large number of the *Canidae*.

The lack of the members of the family *Felidae* is caused by the there prevailing weather conditions, because the *Felidae* are for the most part thermophilous animals. Neither do any species from the other zoogeographical regions reach this province.

2. Boreal Province

This is the largest province of the Holarctic Region, characterized, above all, by extensive wooded areas, the forests being chiefly coniferous. A greater part of the Boreal Province is covered by taiga forests, but there are also mixed and deciduous forests (Europe) and steppes (Area 39 — Transvolga-Kazakh Steppes).

The carnivore fauna is rich and differentiated here, and it includes members of nearly all the families of this order (except for those of the families *Hyaenidae* and *Procyonidae*). Its composition is shown in Fig. 7.

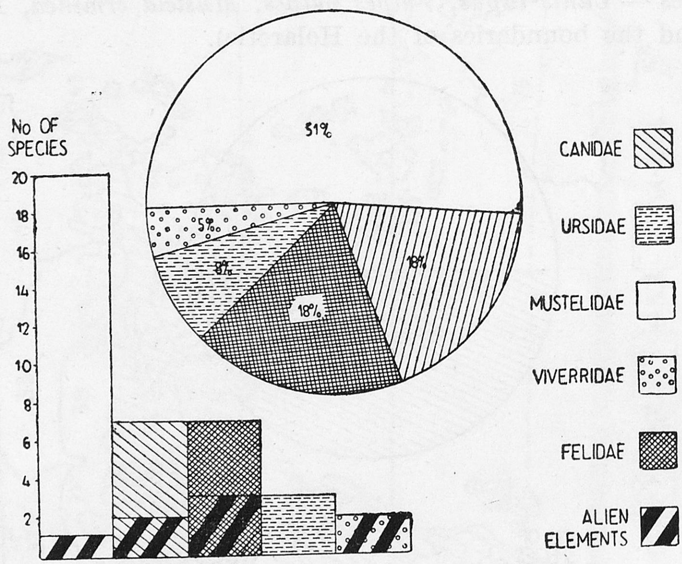


Fig. 7. The fauna of the Boreal Province

The statistical data do not define the actual role of all the families in the given fauna. A high position held by the members of the *Felidae* is connected with the occurrence of such species as *Panthera tigris*, *P. uncia* and *Felis bengalensis* in the south-eastern portion of the Kazakh-Chinese Area, where the northern boundary of their distribution runs, though they are of minor importance in so far as the whole province is concerned. If we left out these species, the family composition would be still more „Holarctic", including the *Mustelidae*, *Canidae* and *Ursidae*. Like the above-mentioned species of the family *Felidae*, the *Viverridae*, too, have their northern range in this province.

The nearly complete lack of endemic species is a characteristic of the Holarctic carnivore faunas. Such forms in the Boreal Province are *Martes zibellina* and *Enhydra lutris*. In modern times the range of *Martes zibellina* has shrunk owing to the activities of man. The occurrence of *Enhydra lutris* is confined to the American and Asiatic coasts of the Pacific Ocean.

The activities of man have caused a radical limitation in the occurrence of a number of the carnivore species, e. g., *Ursus arctos*, *Canis lupus*, *Lynx lynx*, and others.

A great proportion of the carnivores of the Boreal Province are the species which have a very wide range of occurrence, extending beyond the boundaries of the Holarctic Region (15 species, which makes 38 per cent). The share of species from other regions is much lower (18 per cent).

Out of the most numerously represented family *Mustelidae*, the members

of the genera *Mustela* and *Martes* are the commonest. They are typical Holarctic genera.

In some zoogeographical publications the Holarctic is divided into the Palaearctic and Nearctic. I have not used this division in the present study and so I should like to present the facts here which justify my standpoint. Five species of the carnivore fauna of the Boreal Province (13·5 per cent) occur only in the Alasko-Canadian Area (*Canis latrans*, *Ursus americanus*, *Spilogate putorius*, *Lutra canadensis* and *Felis concolor*). They are vicarious species, which have their counterparts in the Old World (*Canis latrans* — *C. aureus*, *Ursus americanus* — *U. thibetanus*, *Spilogate putorius* — *Mustela putorius*, *Lutra canadensis* — *Lutra lutra*). These are for the most part species from the same genera.

In this study I made use of the results obtained by ERDBRINK (1953) on the American form of *Ursus arctos* (so-called grizzly) and WALKER'S opinion (1964) on the forms *Vulpes vulpes* — *V. fulva* and *Lynx lynx* — *L. canadensis.*

In the light of the foregoing data, the division of the Holarctic into the Palaearctic and Nearctic would be quite artificial, especially in so far as the carnivore fauna is concerned (similar situations are found in other mammalian orders).

Most of the carnivore fauna of the Boreal Province consists of forest species or eurybionts, and only some of them (e. g., *Canis aureus*, *C. latrans*, *Vormela peregusna*, *Felis manul*) are associated with steppe environment. *Alopex lagopus* is a tundra species which occurs only in the transitional tundra-forest zone in the northern outskirts of the Boreal Province.

3. Mediterranean Province

This province includes the northern coasts and islands of the Mediterranean Sea, a part of the Iberian Peninsula and the Caucasus. It is not so compact a unit as the previous one. The affinity between the Iberian Area and the Area of the Mediterranean Islands is 75—90 per cent and that between these areas and the Balkan and Caucasian ones only 60—75 per cent. All these areas show an affinity with the particular areas of the Boreal Province, ranging from 60 to 90 per cent. On account of the resemblance of their carnivore faunas and that of their ecological conditions they have been combined to form one province.

Man's interference has influenced the specific composition of the carnivore fauna of the Mediterranean Province in an essential manner, for these are areas that have been witnessing the activities of man for a long time and these activities have brought about a great reduction in the area of woodlands. In historical times, about 2000 years ago, the lion *(Panthera leo)* occurred in Greece. Now, large carnivore species occur quite locally, being confined to the least accessible nooks of this province. The composition of the carnivore fauna is presented in Fig. 8.

The scheme of occurrence of the families is in principle similar to that in the Boreal Province, but the fauna is less numerous. Foreign elements are naturally the *Viverridae* (Iberian and Balkan Areas, species *Genetta genetta* and *Herpestes ichneumon*) and *Canis aureus* and *Panthera pardus*. This last species occurs in the Caucasus. Although the Mediterranean Province neighbours upon the Ethiopian Region, the sea forms a strong barrier preventing the penetration of species from this last region.

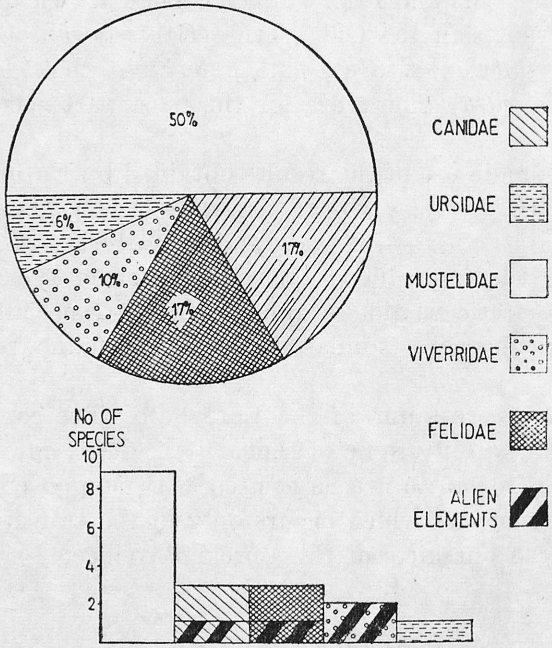


Fig. 8. The fauna of the Mediterranean Province

4. Central Asiatic Province

This province consists of three areas: Tien Shan (53), Tibet (52) and Southern China (50) and, therefore, includes the mountainous massifs of these areas. It borders on the Oriental Region, which has an effect on the specific composition of the carnivore fauna. Fig. 16 shows that 21—30 per cent of the fauna of the South Chinese Area is composed of the Oriental elements.

In the Central Asiatic Province there are some refuges of Tertiary vegetation (mountains of Southern China), with which the occurrence of two procyonid species — *Ailurus fulgens* and *Ailuropoda melanoleuca* — in this territory is connected (this last species is an endemic and inhabits Szechwan only). The *Procyonidae* are an old family, now distributed chiefly in the Neotropical Region.

The composition of the carnivore families of the Central Asiatic Province is given in Fig. 9.

The scheme of occurrence of the families is very characteristic. There are as many as 9 species of the *Felidae* here, of which 6 are of Oriental origin. The foreign elements form 40 per cent of the whole carnivore fauna of this province. There are also 3 widely distributed species of the family *Viverridae*: *Viverricula indica*, *Viverra zibetha* and *Paguma larvata*. The Oriental members of the *Mustelidae* are relatively few, as they embrace only *Arctonyx collaris* and *Melogale moschata*.

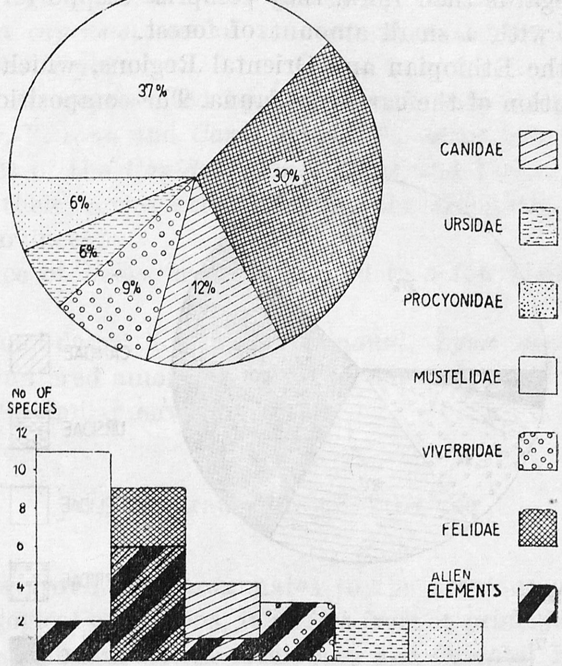


Fig. 9. The fauna of the Central Asiatic Province

The above-mentioned species *Ailuropoda melanoleuca* and *Vulpes ferrilata*, the latter of which occurs only in the Tibetan uplands, are endemic forms.

The fauna of this province is relatively rich, especially in the South Chinese Area (26 species). In the Tien Shan and Tibet Areas there are 12 and 16 species, respectively. The factor responsible for the abundance of the carnivore fauna in the South Chinese Area is the presence of numerous refuges of the Tertiary vegetation, which made it possible for this varied fauna to survive the glaciations. KOSTROWICKI (1969) discussed this problem at length in his publication on the Macrolepidopteran fauna of the Palaearctic Region.

The South Chinese Area shows a 60—75-per-cent affinity with the Himalayan Area of the Oriental Region. It is the only area of this province in which there live some members of the *Viverridae* and Oriental species of the *Mustelidae*. *Cuon alpinus* is an Oriental species widely distributed throughout this province.

Out of the Oriental forms, the *Felidae* are also present in all the areas, but all the six Oriental species of this family occur in the South Chinese Area only.

These facts indicate that the South Chinese Area is a transitional zone between the Holarctic and Oriental.

5. Levanto-Turanian Province

This province has been formed by the combination of 7 working areal units into 6 areas. As regards their flora, they comprise steppe formations, in great part upland ones, with a small amount of forest.

It borders on the Ethiopian and Oriental Regions, which fact also had an effect on the formation of the carnivore fauna. The composition of this fauna is shown in Fig. 10.

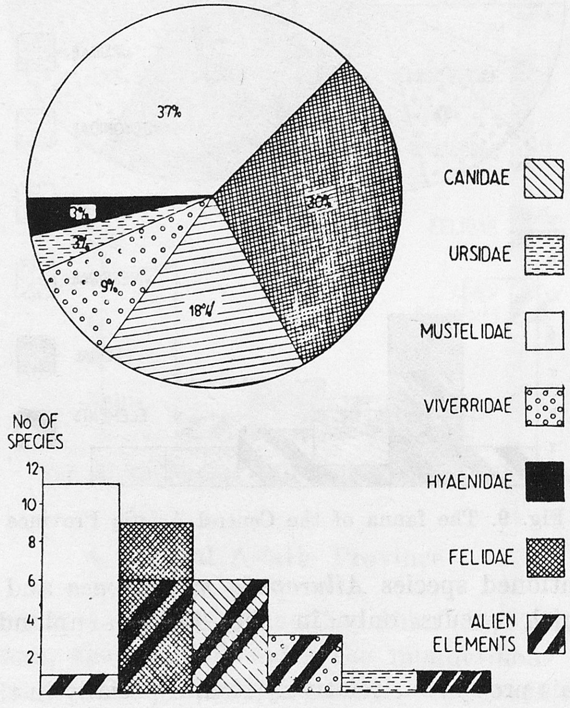


Fig. 10. The fauna of the Levanto-Turanian Province

The scheme of the families of the *Carnivora* in the Levanto-Turanian Province is, at first sight, very similar to that in the Central Asiatic Province, which results from a similar position of this province in relation to the Oriental Region.

An interesting problem is, above all, that of the influence exerted on the fauna under study by the neighbouring faunas and the question which families are the most active in penetration.

In the present case such a family are the *Felidae*. In the fauna examined, as well as in the previous one, 6 species in 9 are foreign elements (*Felis manul*, *Lynx lynx* and *Panthera uncia* are Holarctic species; the remaining ones — *Felis margarita*, *F. chaus*, *F. libyca*, *Panthera pardus*, *Lynx caracal* and *Acinonyx jubatus* — are Oriental or Ethiopian forms).

Another family of penetrant forms are the *Viverridae*; their species, *Herpestes ichneumon*, *H. auropunctatus* and *H. edwardsii*, have wide ranges, similarly to the only member of the *Hyaenidae*, *Hyaena hyaena*.

Only one foreign form is met with among the *Mustelidae*, the Ethiopian species *Mellivora capensis*, one of the two most eurytopic Ethiopian forms (the other is *Felis libyca*).

The *Canidae* are represented by steppe and semi-desert species — *Vulpes rupelli*, *V. corsac*, *V. cana* and *Canis aureus*, *V. corsac* being an endemic form. The other species of the *Canidae*, *Canis lupus* and *Vulpes vulpes*, are widely distributed and their ranges extend beyond the Holarctic into the Ethiopian and Oriental Provinces.

The occurrence of *Ursus arctos* is limited to a few mountainous forests of this province.

The steppe-semi-desert forms, *Felis manul*, *Lynx caracal* and *Acinonyx jubatus*, are encountered among the *Felidae*. The occurrence of *Hyaena hyaena* is associated with similar environments.

6. Arabo-Punjab Province

Although this province approximates to the previous one in geographical position and ecological conditions, it differs from it principally in its carnivore fauna. It, too, neighbours on the Ethiopian and Oriental Regions, which fact finds its reflection in the composition of the carnivore fauna, presented in Fig. 11.

The scheme of the families in this province is entirely different from that of the other provinces of the Holarctic Region. The *Felidae*, which have not a single Holarctic species, are placed first. The *Canidae* and *Mustelidae* have one foreign species each, *Fennecus zerda* and *Mellivora capensis*. There appear numerous viverrids. They number 5 species, of which only one (*Genetta genetta*) is of Ethiopian origin. Most foreign elements (two-thirds) are of Oriental origin. Sixty per cent of the carnivore fauna of this province is of foreign origin.

A zoogeographical curiosity is the relict locality of *Panthera leo* at Gir Pahadiyan, Kathiyavar, at present the only one in Asia. In historical times the lion lived throughout Asia Minor, Arabia, Palestine and Syria (Darlington, 1957).

The affinities of this province with the areas of the Ethiopian Region are rather low, below 60 per cent, reaching the level of 60—75 per cent only with

the Sahara and Yemen Areas. It shows the same level of affinity with the Central Indian Area of the Oriental Region and with the Levanto-Turanian Province. These data indicate a transitional character of this province.

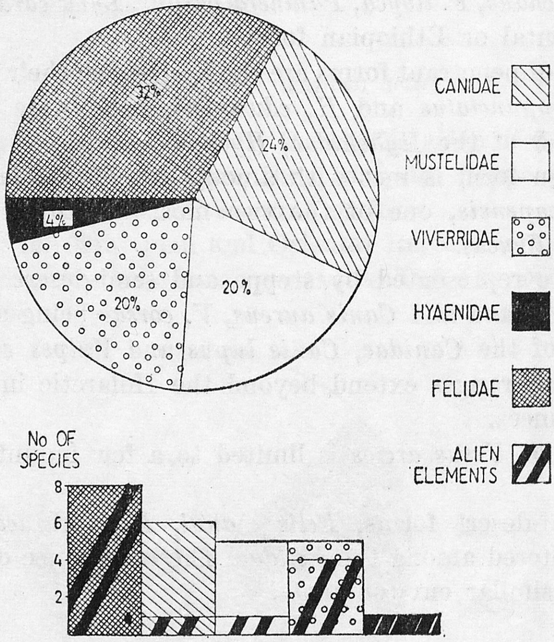


Fig. 11. The fauna of the Arabo-Punjab Province

7. American Province

This province comprises the central and southern parts of the North American continent, contiguous to the Boreal Province on the north and the Neotropical Region on the south. The geographical position of this province has a decisive effect on the composition of the carnivore fauna (CAHALANE, 1947; HALL and KELSON, 1959; MILLER and KELLOGG, 1955). The composition of the carnivore fauna is given in Fig. 12.

Gradual appearance of Neotropical genera and species may be observed in particular areas, from the north southwards. The composition of the carnivore fauna, presented in the graph, has been strongly influenced by the fauna of the Sonoran Area, in which the share of Neotropical elements reaches 30 per cent (Fig. 25). In the other areas the share of these elements does not exceed 10 per cent. It should be emphasized here that there is a well-defined boundary, beyond which the Neotropical elements never go, namely, the boundary of the Boreal Province. Forests of the taiga type occur in this province in North America and the Neotropical elements do not find favourable living conditions in them.

The Neotropical carnivore fauna (see p. 344) is very specific. A great adaptation to definite environmental conditions has taken place in this territory and

there is an abundance of species here, which are, however, markedly stenobiotic species. On the other hand, the Holarctic members of the *Carnivora* are on the whole much more eurybiotic.

The fauna of the American Province is not very numerous and four groups of species can be distinguished in it:

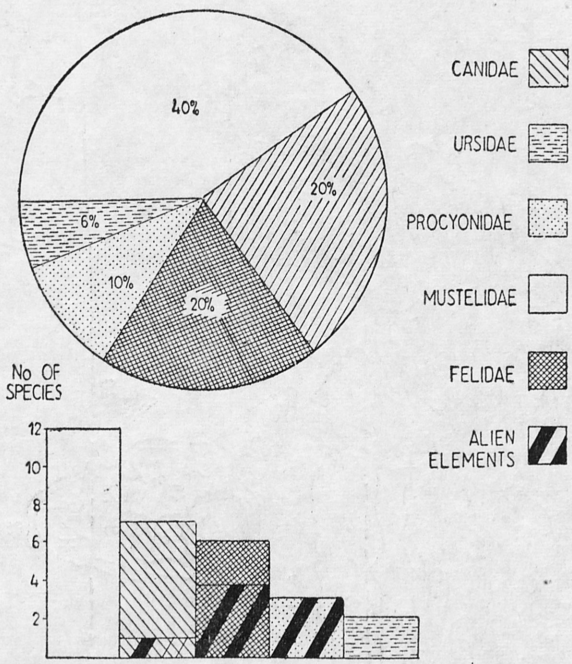


Fig. 12. The fauna of the American Province

1. Widely distributed Holarctic species: *Canis lupus*, *Vulpes vulpes*, *Mustela erminea*, *M. vison*, *Ursus arctos*;
2. Endemic and vicarious species: *Vulpes macrotis*, *V. velox*, *Urocyon littoralis*, *Mustela nigripes*, *Martes pennanti*, *Mephitis mephitis* (endemic species of this province) and *Canis latrans*, *Ursus americanus*, *Taxidea taxus*, *Lutra canadensis* (vicarious species);
3. Widely distributed North American species: *Mustela frenata*, *Spilogale putorius*, *Felis concolor*, *Lynx rufus*;
4. Neotropical eurytopic species: *Urocyon cinereoargenteus*, all *Procyonidae*, *Mephitis macroura*, *Conepatus mesoleucus*, *Panthera onca*, *Felis pardalis*, *F. wiedi*, *F. yaguaroundi*.

The American Province has been formed of 11 working area units and constitutes a very heterogeneous territory both in geographical and in geobotanical respect, including coniferous and mixed forests of the northern part of the United States as well as prairies, mountains and even subtropical formations (Florida); however, it has a relatively uniform carnivore fauna so far as

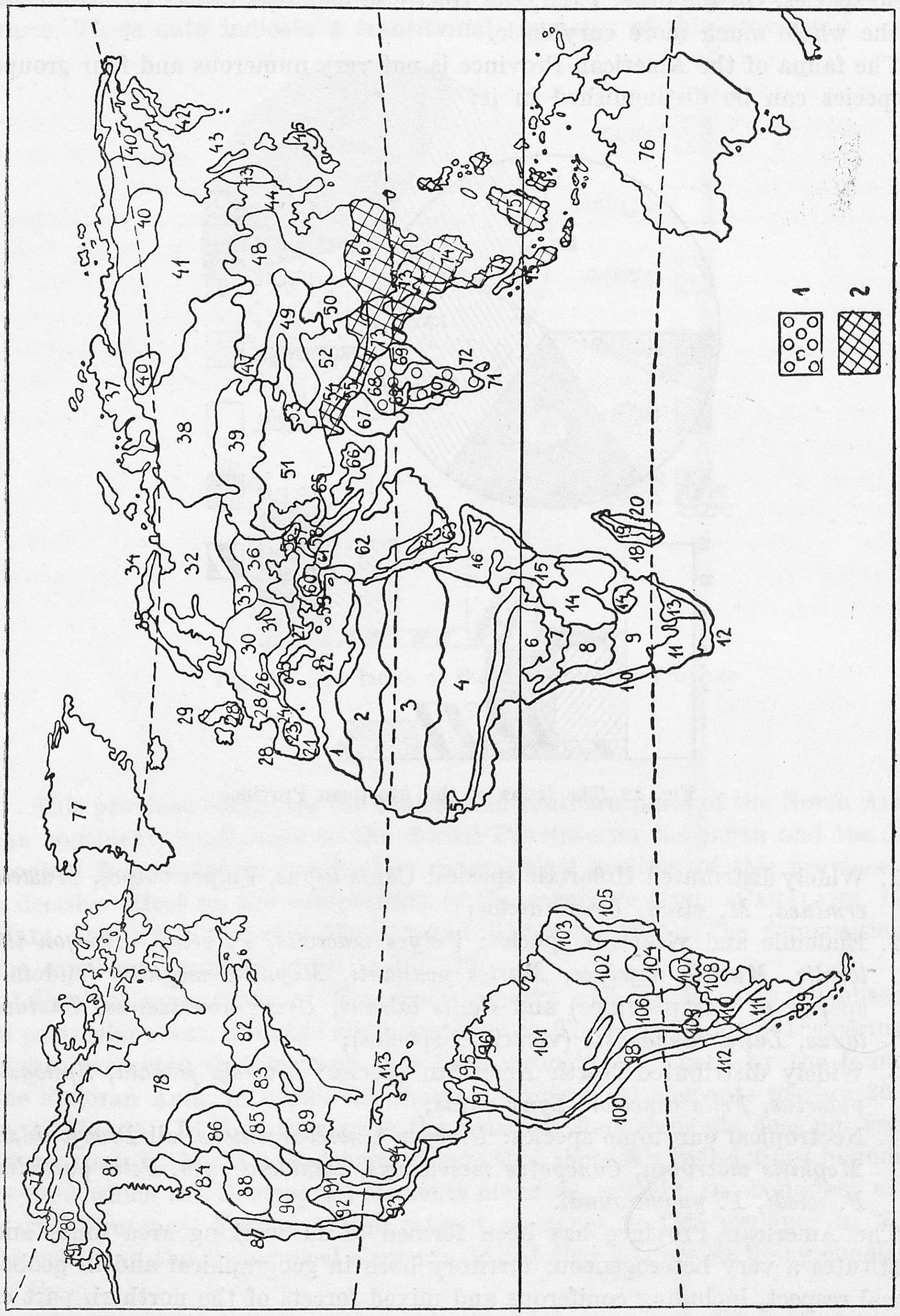


Fig. 13. Provinces of Oriental Region

its specific composition is concerned, which caused the combination of so many units into one province.

The tracing out of the boundary between the Holarctic and the Neotropical Region is a controversial problem. In the light of the data concerning the carnivore fauna the Sonoran Area, embracing the southern uplands of the United States and northern Mexico, is the last Holarctic Area. Most species of the fauna of this Area are Holarctic species (about 70 per cent), which also have the southern boundary of their distribution here. Only a few Holarctic species have their ranges extending beyond this boundary (*Canis latrans*, *Mustela frenata*, *Felis concolor*, *Lynx rufus*). The now prevailing weather and floral conditions in Central America appear to form a barrier which is impassable for most Holarctic species.

On the other hand, it has recently been observed that the Neotropical forms (e. g., *Urocyon cinereoargenteus*) rapidly shift the boundary of their distribution farther to the north.

II. Oriental Region

With regard to its flora the Oriental Region comprises various tropical and subtropical formations, savannas, deserts, and mountainous formations. The relatively large number of endemic forms occurring in this Region, both genera and species, is connected with the great diversity of environmental conditions and the presence of islands.

The data concerning the carnivore fauna can be found, among other publications, in those by ALLEN (1938—40), CHASEN (1940), ELLERMAN and MORRISON-SCOTT (1951), TATE (1947) and WALKER (1964).

The Oriental Region has been divided into two provinces, the Sino-Malay and the Indian, which show essential differences in the carnivore fauna.

1. Sino-Malay Province

This province, contiguous to the Holarctic Region, has the most abundant carnivore fauna — 56 species — of all the provinces. Its composition is given in Fig. 14.

The carnivore fauna of this province contains many forms which are confined in their ranges to its territory only, often even to only one area. Such species are 19 (34 per cent). Eight genera (belonging to the *Mustelidae* and *Viverridae*) also pertain to this province alone.

The species which occur only in the Sino-Malay Province are *Ursus malayanus* (*Ursidae*), *Mustela strigidorsa*, *Mydaus javanensis*, *Suillotaxus marchei*, *Melogale orientalis*, *Lutra sumatrana*, *Melogale personata* (*Mustelidae*), *Viverra tangalunga*, *Prionodon linsang*, *Macrogalidia mussechenbroecki*, *Arctictis binturong*, *Hemigalus derbyanus*, *Diplogale hosei*, *Cynogale bennetti*, *Chrotogale owstoni* (*Viverridae*), *Felis marmorata*, *F. minuta*, *F. badia* (*Felidae*).

Only ten species are of Holarctic origin; they are widely distributed and form about 18 per cent of the fauna examined. There is hardly one Ethiopian species, *Mellivora capensis*. The family *Ursidae* is represented fairly numerously by *Ursus thibetanus* and two Oriental species: *Ursus malayanus* and *Ursus ursinus* (according to the taxonomy given by ERDBRINK, 1953).

The fauna of the Indonesian Islands and Philippines contains several species which occur only in this area: *Mydaus javanensis* lives on Borneo, Java and Sumatra, *Suillotaxus marchei* on the Palawan and Calamian Islands near Borneo, *Melogale orientalis* on Java and Borneo, *Lutra sumatrana* on Sumatra, *Viverra*

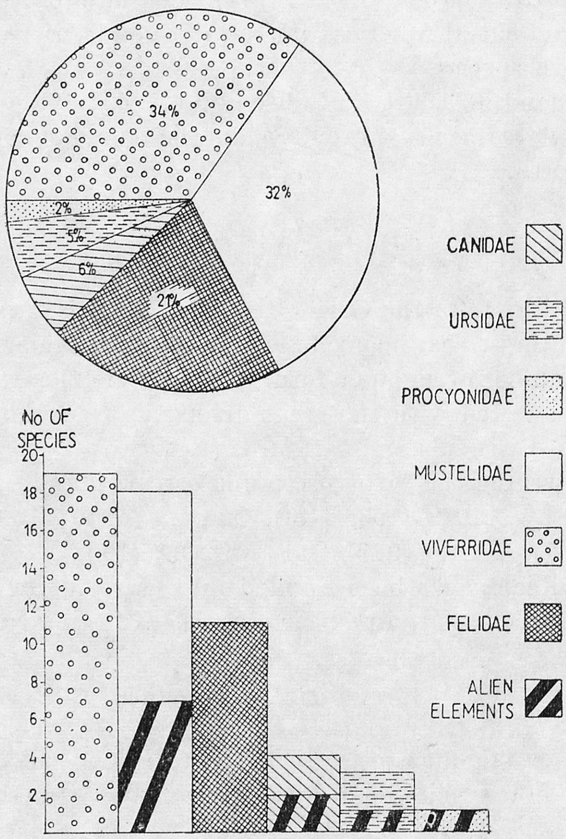


Fig. 14. The fauna of the Sino-Malay Province

tangalunga in Eastern India and Philippines, *Macrogalidia mussechenbroecki* on Celebes, *Diplogale hosei* on Borneo, *Felis minuta* on the Philippines and *Felis badia* on Borneo.

A specific nature of this province is indicated by the fact that its affinities with the areas of the neighbouring Indian Province do not exceed 60—72 per cent.

Its fauna is completely different in character from the faunas of the provinces of the Holarctic Region (Figs. 6—12), since it shows a clear predominance

of the members of the family *Viverridae* and so may be defined, together with the other Oriental and Ethiopian faunas (except that of the North African — Yeman Province, which will be discussed below), as a „viverroidal" one, whereas the carnivore faunas of the Holarctic and Neotropical Regions are „musteloidal".

I shall deal with the general character of the faunas in the final part of this paper.

Although the Sino-Malay Province borders on the Holarctic Region, the influence of this last on the specific composition of the carnivore fauna is slight. The boundary between these Regions is distinct, it runs in the Southern Chinese Area, which is, as I have stated above, a transitional zone.

2. Indian Province

This province embraces a greater part of the Indian Peninsula and Ceylon. The composition of its carnivore fauna is presented in Fig. 15.

In the west it neighbours on the Punjab Area of the Holarctic Region. The share of the Holarctic elements is slight — only *Canis lupus* and *Lutra*

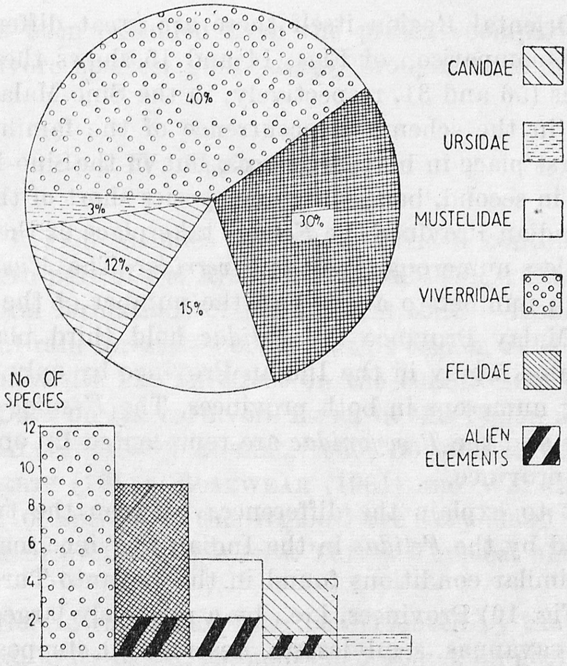


Fig. 15. The fauna of the Indian Province

lutra — though there are no barriers to stop the Holarctic species from penetrating into it. The species of Ethiopian origin are somewhat more numerous, they include *Mellivora capensis*, *Felis libyca* and *Acinonyx jubatus*.

The fauna of this province is, as has already been stated in general for the carnivore faunas of the Oriental and Ethiopian Regions, „viverroidal" in character. There are comparatively many forms, about 24 per cent of the total,

restricted to this single province. These species are: *Vulpes bengalensis*, *Martes gwatkinsi*, *Paradoxurus jerdoni*, *P. zeylonensis*, *Felis rubiginosa* and *F. planiceps*. Only one form, *Paradoxurus zeylonensis*, is an insular species from Ceylon.

The carnivore fauna of Ceylon very much resembles that of the other areas of this province. It comprises only one non-Oriental species, *Lutra lutra*.

The closest affinities shown by the Indian Province are those with the Himalayan and Indonesian-Philippine Areas (60—75 per cent) and with the Syrian Area (61) of the Arabo-Punjab Province of the Holarctic Region.

As will be seen from the foregoing review, the Oriental Region has a specific carnivore fauna, which, in spite of the lack of geographical barriers in the east and west, is only to a low degree penetrated by Holarctic species (within limits of 6—18 per cent). This is especially true of the Indian Province, in which the Holarctic species constitute hardly 6 per cent of the fauna. The Punjab Area appears to be this very transitional zone, the „filter" that stops the Holarctic species. In this area the Holarctic species form 25 per cent and the Oriental ones 50 per cent of the carnivore fauna (the remaining species are of Ethiopian origin).

Within the Oriental Region itself there are great differences between its two provinces. A comparison of Figs. 14 and 15 shows them not only in the number of species (56 and 31, respectively, in the Sino-Malay and Indian Provinces) but also in the scheme of occurrence of the families. The *Viverridae* naturally hold first place in both provinces, but in the Sino-Malay Province the *Mustelidae* come in second, being only one species short of the previous family, whereas in the Indian Province the *Felidae* take place of the *Mustelidae*, being only 25 per cent less numerous than the *Viverridae*. The *Mustelidae* follow them and they equal in number to about half the number of the *Felidae*.

In the Sino-Malay Province the *Felidae* hold third place, exceeding the number of the same family in the Indian Province by only 2 species. The *Canidae* are equally numerous in both provinces. The *Ursidae* have already been mentioned above and the *Procyonidae* are represented by one species *(Ailurus fulgens)* in this province.

It is difficult to explain the differences between the two provinces. The high position held by the *Felidae* in the Indian Province may be explained by analogy to the similar conditions found in the Levanto-Turanian (Fig. 9) and Arabo-Punjab (Fig. 10) Provinces, i. e., by a relatively large number of similar environments — savannas, semi-deserts, deserts and steppes — which provide biotic conditions suitable for most members of the family *Felidae*. This explanation is only partly convincing, because in the Congolese Province (Fig. 16) the scheme of occurrence of the families is identical, though the environmental conditions are quite different (I shall still return to this problem in this paper).

I think, however, that the occurrence of the large number of species of the family *Felidae* may be explained by the above-mentioned environmental conditions. The *Felidae* have lived in Asia since the Pliocene, in Africa they appeared as late as the Pleistocene (DARLINGTON, 1957).

Fig. 16 shows the ranges of the Oriental elements. However, their extensiveness (they cover the whole Ethiopian Region and a large part of the Holarctic) is due to the occurrence of only 3 species of Oriental origin, *Canis aureus*, *Cuon alpinus* and *Panthera pardus*. *Canis aureus* is a typical steppe-desert form, *Cuon alpinus* is rather associated with forest formations. *Panthera pardus* is a remarkably eurybiotic species (*Felis concolor* plays the same role in the regions of the New World).

The share of the Oriental members of the *Mustelidae* and *Viverridae* is restricted to the adjacent provinces.

The Oriental Region is relatively more intensely penetrated by Holarctic species than the Holarctic Region by the Oriental ones (in absolute numbers). This is particularly true of the Sino-Malay Province, which is penetrated, above all, by the Holarctic members of the *Mustelidae*.

III. Australian Region (76)

This region has been excluded from the present comparisons, because it has only one carnivore species, *Canis dingo*, brought to it by man.

IV. Ethiopian Region

The Ethiopian Region includes the whole African continent, Madagascar and the south-eastern part of the Arabian Peninsula (Figs. 3 and 17). Virtually all the types of floral formations of the tropical zone — from deserts through savannas to tropical rain forests — occur in this region. It is largely differentiated, which undoubtedly has an effect on the composition of the carnivore faunas examined. Data on the carnivore fauna in this region are given, among other authors, by Allen (1939), Ansell, 1960; Bourlière (1962), Ellerman et al. (1953), Roberts (1951), Rosewear (1961) and Walker (1964).

A large number of species of this region have very small ranges, confined to a single province or even a single area. This is a typical phenomenon of the tropical zone.

The differentiation of this region may be evidenced by the fact that nearly all the working areal units based, as mentioned above, on geobotanical criteria were preserved when put to statistical analyses.

The diagram shows a distinct mosaic arrangement of particular areas, which differ from each other markedly, as reflected by the affinities between them, ranging from 60 to 75 per cent and often being even lower.

The most compact zoogeographical units are indubitably the Malagasy Province, which reveals hardly any affinities to the other areas of the region, and the North African and Yemen Areas. These two areas have been combined into the North African-Yemen Province.

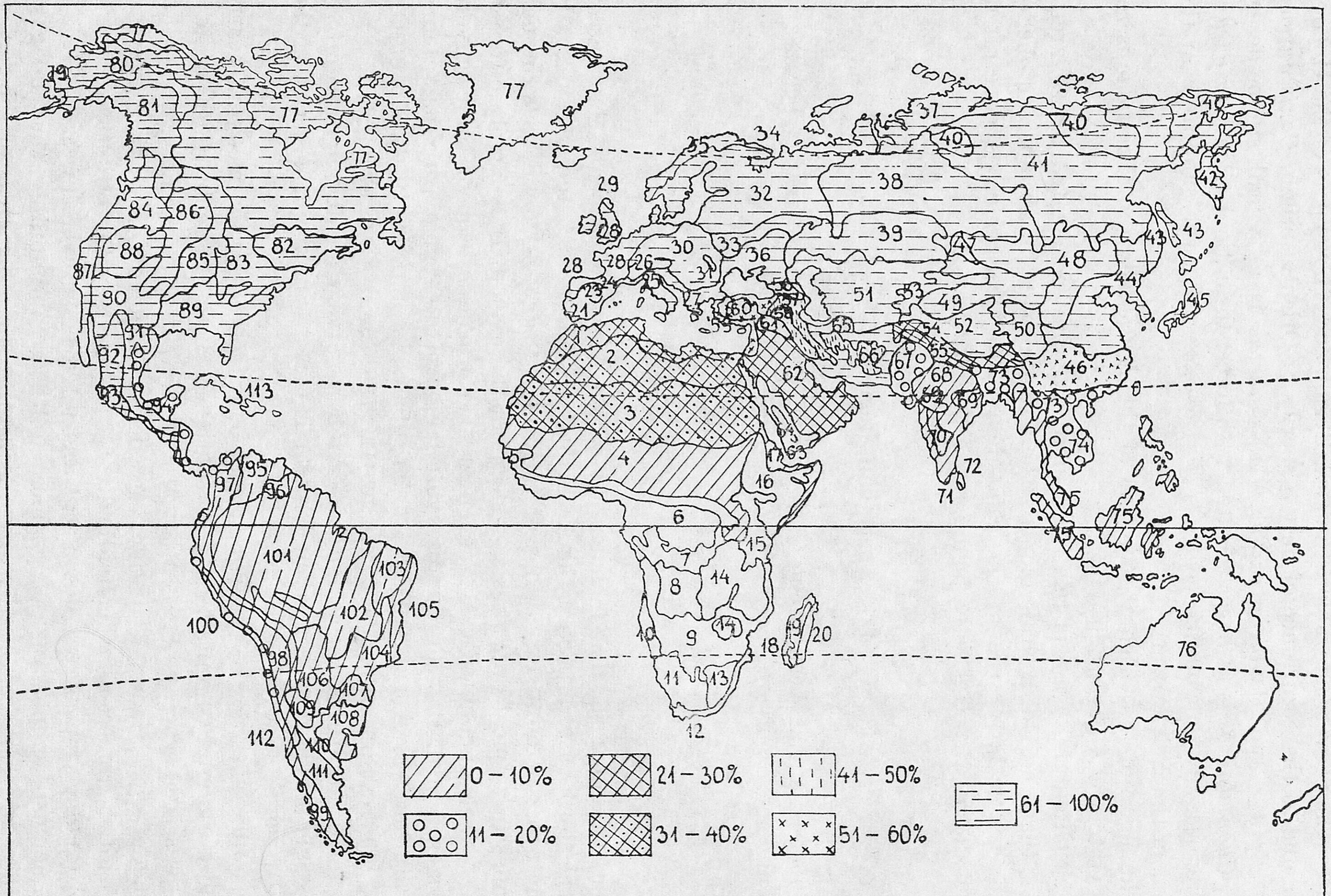


Fig. 16. The share of the Oriental elements

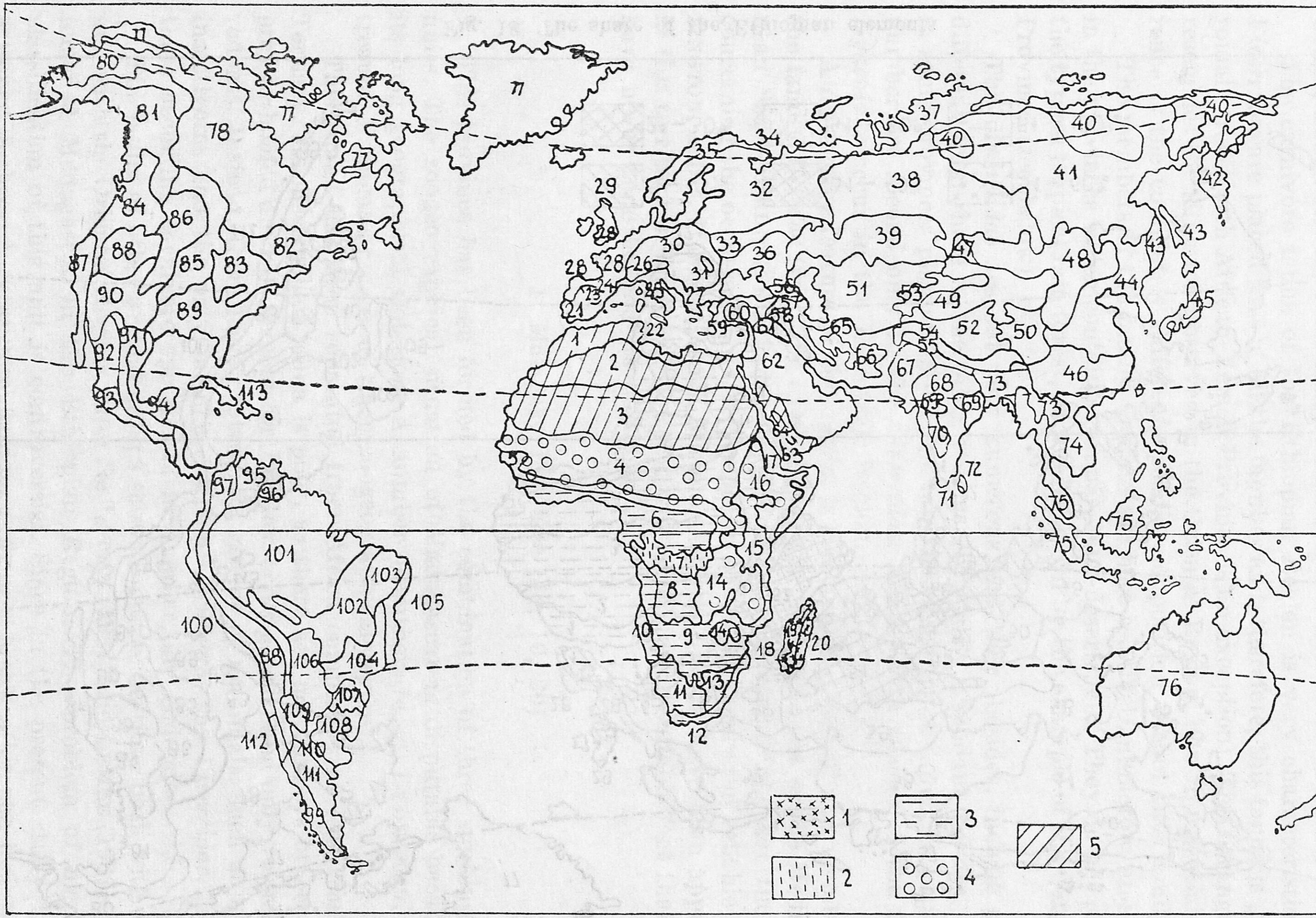


Fig. 17. Provinces of the Ethiopian Region. 1 — Malagasy, 2 — Congolese, 3 — South African, 4 — East African, 5 — North African—Yemen

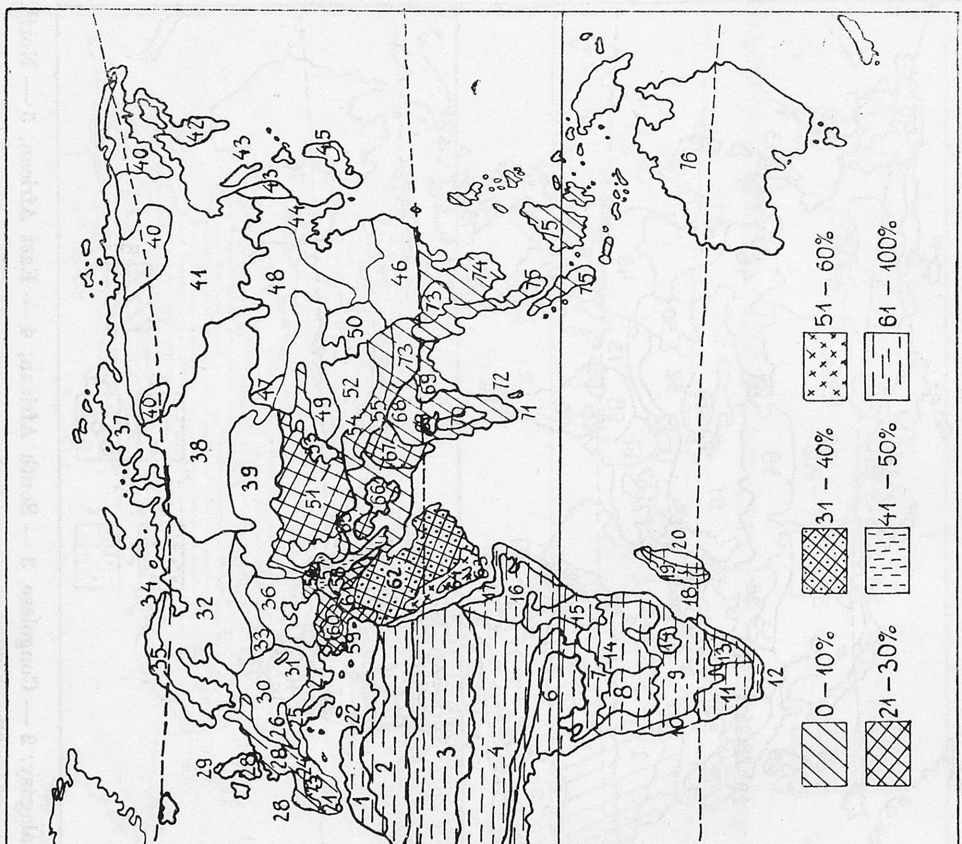


Fig. 18. The share of the Ethiopian elements

The Ethiopian Region has been divided into five provinces (Madagascar, Congo, South Africa, East Africa, and North Africa with Yemen).

The carnivore fauna of the Ethiopian Region is very characteristic. The *Viverridae* are placed first of all the families and, therefore, this fauna is „viverroidal“ (the North African-Yemen Province is an exception). This arrangement resembles the situation observed in the Oriental Region, but an essential difference is the completely different specific composition within this family.

The members of the family *Canidae* are here relatively numerous and occur in the provinces which contain savannas, semi-deserts, etc. They do not inhabit the typical tropical rain forest, as will be shown by the example of the Congolese Province (see below).

The *Mustelidae* are not very numerous and they, besides, include genera different from those in the other regions. The fairly abundant *Felidae*, which in some provinces play an important role in the carnivore fauna, in respect of number are second only to the *Viverridae*. All the four species of the family *Hyaenidae* occur in the Ethiopian Region.

A distinctive feature of this region is the complete lack of any members of the family *Ursidae* (with the exception of the African coasts of the Mediterranean Sea — ERDBRINK, 1953). Some authors, however, think that the data concerning the occurrence of the *Ursidae* in North Africa are not reliable (DARLINGTON, 1957). If we, after all, assume that the *Ursidae* have been appearing in this territory in historical times, it will remain an irrefutable fact that they have never gone beyond its boundary.

1. Malagasy Province (18, 19, 20)

This province has been formed by the combination of three working areal units. The zoogeographical situation of Madagascar is disputable because of its long geographical isolation. A number of authors (e. g., LYDEKKER, 1896) treated Madagascar as a distinct zoogeographical region.

This island has been separated from Africa completely at least since the Tertiary. Its mammalian fauna is poor, as there are no monkeys or beasts of prey or hoofed animals (except for *Potamochoerus porous*) and only very scanty rodents. Instead, there have evolved old groups of mammals, such as lemurs, insectivores and the only members of the *Carnivora*, the *Viverridae*. All the there occurring carnivore species, 12 in number, are endemic.

The fauna of other animal groups shows some connections both with Africa and with the Oriental Region. After De LATTIN (1967) and LEMEE (1967) I have included Madagascar in the Ethiopian Region. The problem of hierarchic classification of this unit is controversial. Since in the present study I have assumed a three-stage system (region, province, area), after the inclusion of Madagascar in the Ethiopian Region I must classify it as a province, though in a more well-developed hierarchy it would rank higher.

2. Congolese Province (7)

This province contains only one area, the Congolese one (7). The diagram shows that its position is largely isolated. Its affinities reach 60—75 per cent only in relation to the Equatorial Area of the South African Province, being quite low in relation to the other areas.

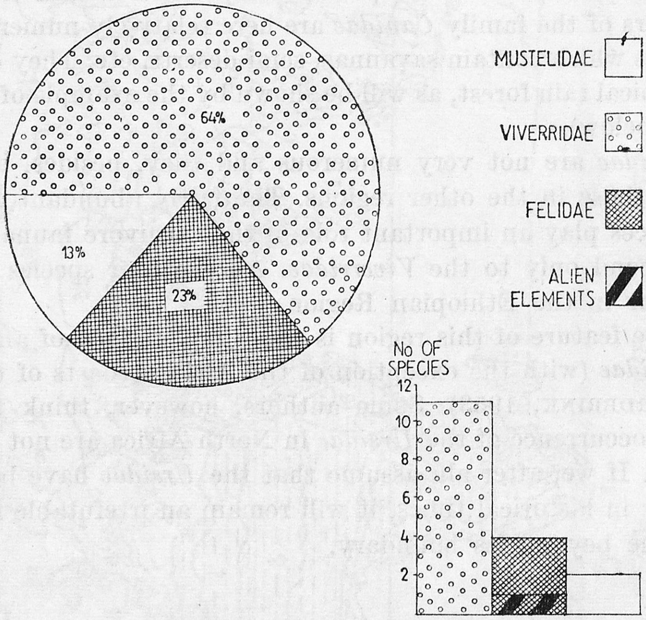


Fig. 19. The fauna of the Congolese Province

The Congolese Province embraces the formations of evergreen forests with variable humidity (this is the zone of rainy season). The enormous richness of tree species, the development of specific adaptations, and the great closeness and multilayered structure of forests, with the ever-prevailing dusk at their floor are characteristics of these forests. This kind of environment has an evident influence on the carnivore fauna (Fig. 19).

As will be seen from Fig. 19, the carnivore fauna of this province is quite specific. The lack of the families *Canidae* and *Felidae*, associated generaly with open areas as manifested by their manner of getting food, is obvious. The only big carnivore is the Oriental species *Panthera pardus*, an eurytopic form, which in this province finds similar conditions to those in the damp forests of India or the Malay Peninsula, the other species being as a rule small forms.

There are two endemic species of the *Viverridae*, *Osbornictis piscivora* and *Xenogale microdon*.

3. South African Province

This is a comparatively large province consisting of 7 areas. It is markedly differentiated geobotanically, as it includes deserts, semi-deserts, savannas, parklands, and dry and damp tropical forests. In spite of such differentiation found in this province its carnivore fauna is distinct in character, quite different from the faunas of the remaining provinces (Fig. 20).

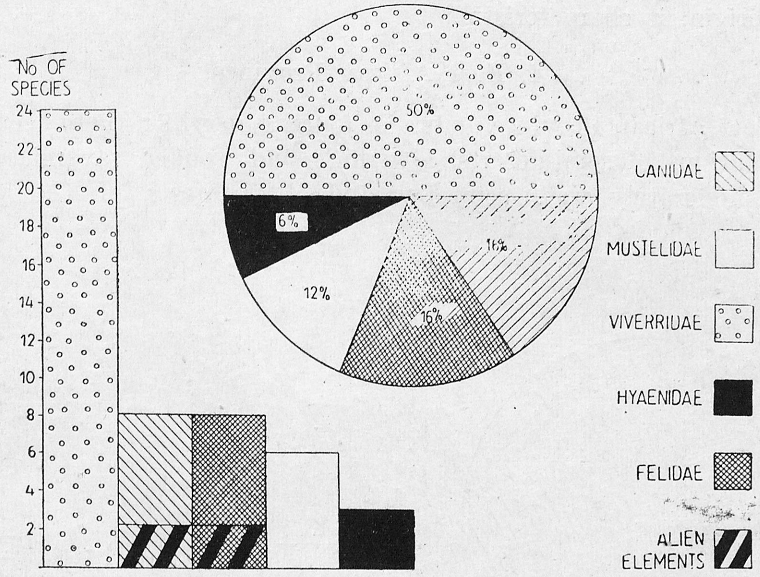


Fig. 20. The fauna of the South African Province

It is highly „viverroidal" (50 per cent), whereas the *Canidae* and *Felidae* equal in number, come next in this respect. Nearly all genera of the *Viverridae* are typically Ethiopian (except the genus *Herpestes*). The species which are confined to this province alone are relatively numerous and form 28 per cent of the fauna. Their number may be rather due to the poor knowledge of the taxonomy of a given genus or family (the *Viverridae* comprise 10 such species) than to the actually existing diversity of forms (which, however, cannot be excluded). For instance, out of the 7 species of the genus *Herpestes* occurring in this province, 5 are limited exclusively to its territory. Nevertheless, having no adequate materials for comparison, I simply had to base myself on the data from literature and, for this reason, I can only surmise that some subspecific forms have been described as distinct species.

The forms whose occurrence is confined to this province are: *Vulpes chama (Canidae)*; *Paraonyx microdon (Mustelidae)*; *Genetta lehmani*, *Liberiictis kuhni*, *Suricata suricatta*, *Herpestes cauui*, *H. pulverulentus*, *H. ratlamuchi*, *M. ignitus*, *H. nigratus*, *Cynictis penicillata*, *Bdeogale jacksoni (Viverridae)*; *Hyaena hyaena (Hyaenidae)*; *Felis nigripes (Felidae)*.

The large number of the *Canidae* indicates the existence of open areas in this province. There are also two Ethiopian genera, *Lycaon* and *Otocyon* (species *Lycaon pictus* and *Otocyon megalotis*), in it. The occurrence of the species *Lynx caracal* and *Acinonyx jubatus* and of three members of the family *Hyaenidae* in this province is also connected with the presence of savanna and semi-desert environments.

The low share of foreign elements (8 per cent), which are exclusively of Oriental origin, is characteristic.

4. East African Province

The East African Province embraces 6 areas, in which there occur geobotanical formations of semi-deserts, low, high and wooded savannas, bush and tropical - moderately wet, semi-dry and dry - forests of the park type.

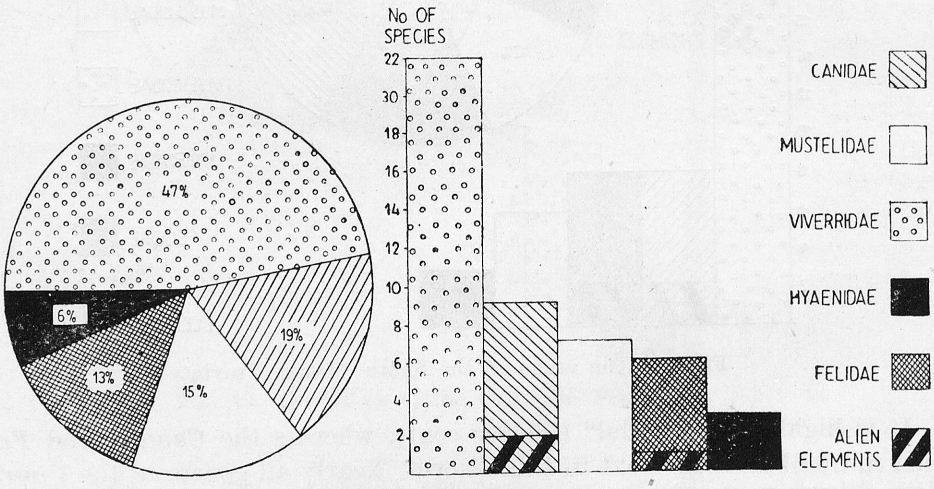


Fig. 21. The fauna of the East African Province

The environmental conditions have a distinct effect on the carnivore fauna, the composition of which is shown in Fig. 21.

A comparison of Fig. 21 with the previous one shows clear-cut differences. Although both the faunas are of the „viverroidal" type and in both the *Canidae* come in second, in the East African Province the *Felidae* are replaced by the *Mustelidae*. The *Hyaenidae* come in last in both these provinces.

The *Canidae* include *Vulpes vulpes*, the only Holarctic form met with south of the Sahara.

The occurrence of *Acinonyx rex* in Rhodesia, which differs from *A. jubatus* in being striped instead of spotted, is a controversial question. This species was described on the basis of several specimens in 1927. I assume, after WALKER (1964), that it is only a local variety of the cheetah.

Another difference is the small number of species which are confined to only

one province. It comes to less than half the number of such species in the previous province (6 against 14).

The foreign elements are still fewer, hardly 6 per cent.

The *Canidae*, containing the species *Fennecus zerda*, reveal an influence of the deserts. In the *Hyaenidae*, represented, as in the previous province, by 3 species, the widely distributed species *Hyaena hyaena* appears in the place of *Hyaena brunnea*, which occurs only in the South African Province.

5. North African-Yemen Province

This province, being the last of the Ethiopian Region, has been formed of 5 working areal units combined into two areas, the North African (1, 2, 3) and the Yemen (63, 64).

The North African Area, which is undoubtedly a transitional zone between the Holarctic and Ethiopian Regions, is usually numbered in the first of these two regions. The inclusion of this area in either region depends closely on the animal group on which the division is based.

According to LEMEE (1967), who quotes HEIM de BALZAC, „the mammals which inhabit the Sahara are in the light of all the data available, of tropical, above all, Ethiopian origin“. This is also true of birds. LEMEE next mentions the *Coleoptera*, which, as demonstrated by P. de PEYERIMHOFF, refer the Sahara to the Holarctic. The *Orthoptera* and *Lepidoptera* (KOSTROWICKI, 1965) indicate similar relations of the Sahara to this last region. KOSTROWICKI found this area to be related much more closely to the Europeo-Siberian areas than to the Ethiopian Region.

The North African-Yemen Province comprises desert and semi-desert floral formations except for the narrow coastal zone in North Africa, where the plant formations represent the Mediterranean type.

The results of the present study show unambiguously that so far as the *Carnivora* are concerned this province should be included in the Ethiopian Region, though there are some differences both in the order of occurrence of the families and in the composition of their genera. These data are presented in Fig. 22.

LEMEE, whom I have cited above, combined the North African-Yemen and Arabo-Punjab Provinces, distinguished in this paper, into one unit, the Sahara-Sindian Region (the term „region“ used by that author naturally differs in meaning from that applied in the present study).

The carnivore fauna of the North African-Yemen Province is „musteloidal“ in character and in its family composition resembles the fauna of the Levanto-Turanian Province (Fig. 10). (The fauna of the Arabo-Punjab Province is completely different). In the province under discussion there are only 3 species of the *Viverridae*, of which two *(Genetta genetta* and *Herpestes ichneumon)* have ranges extending far beyond the boundaries of the Ethiopian Region.

Next, as many as 50 per cent of the *Mustelidae* are foreign elements of Holarctic origin *(Mustela erminea, M. nivalis, M. putorius, Lutra lutra)*. Holarctic and Oriental forms *(Vulpes vulpes* and *Canis aureus*, respectively) are also met with among the *Canidae*.

The diagram shows that this province has the highest affinities with the Central African (75—90 per cent), East African and Equatorial Areas of the Ethiopian Region and the Arabian Area of the Holarctic Region (60—75 per cent). As I have already stated, this last area is also transitional in character, just as the whole Arabo-Punjab Province is.

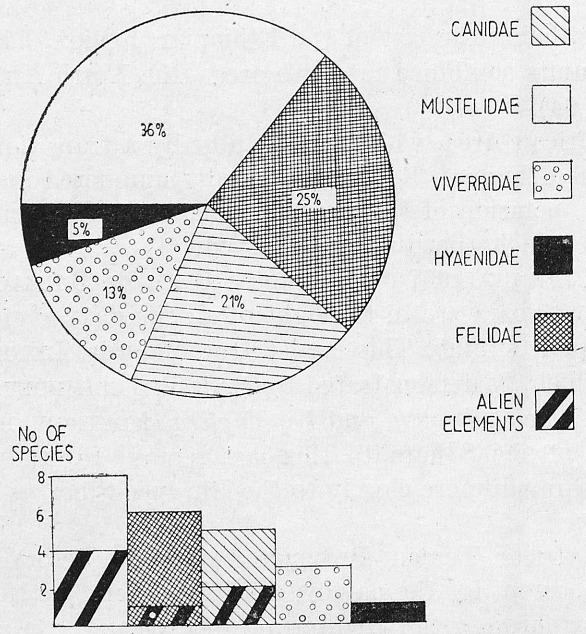


Fig. 22. The fauna of the North-African-Yemen Province

Out of the species occurring in this province, that of the *Ursidae* has already been discussed as a controversial problem. The occurrence of the species *Panthera leo* is now also of historical significance, since in Africa it was exterminated at the turn of the nineteenth century.

The transitional nature of this province may also be supported by the fact that 30 per cent of the species are of foreign origin (but only 17 per cent of Holarctic origin).

In the light of the foregoing data the inclusion of this province in the Ethiopian Region, as a transitional zone, seems well grounded.

V. Neotropical Region

This region occupies the whole continent of South America, from Central America to Patagonia, including a number of very various geobotanical formations, from tropical rain forests to alpine, desert or subantarctic formations.

The mammalian fauna is highly differentiated, which results, among other things, from the long isolation of this continent (before the Pliocene North America had 27 families of mammals and South America 29, none of which was common to both; in the Pleistocene there were 22 common families, of which 14 of North American origin — SIMPSON, after LEMEE, 1967). The order *Edentata*, encountered nowhere outside the Neotropical Region, occurs in South America.

A number of Holarctic forms (*Panthera onca*, *Felis concolor*, *Ursus ornatus* and others) have encroached upon the territory of the Neotropical Region since the junction of both Americas in the Pliocene.

They are at present completely Neotropical forms (except for *Felis concolor*), which do not occur in the Holarctic Region. In the present paper, which deals with the contemporary distribution of carnivores, these species are, therefore, regarded as Neotropical in spite of their Holarctic derivation.

The specific environmental conditions and their enormous diversity caused the formation of a number of species which, for the most part, have no counterparts in the Holarctic carnivore fauna. Here I have based myself chiefly on the publications by CABRERA (1957), CABRERA and JEPES (1960), OSGOOD (1943) and WALKER (1964).

In the Neotropical Region there live a number of carnivore genera which in the American Province of the Holarctic Region occur only in the transitional zone, the Sonoran Area (e. g. the genera *Bassariscus* and *Nasua*). A common character of all the provinces of the Neotropical Region is the low share of the contemporary Holarctic forms, which make 7—8 per cent of its fauna. This is not the case as regards the Antillean Province, where the carnivore fauna is extremely poor and has no species (only genera) in common with the Neotropical Region.

On the basis of a statistical analysis the Neotropical Region has been divided into 4 provinces, the Guyano-Brazilian, the Andean, the Patagono-Andean and the Antillean (Fig. 23).

The Guyano-Brazilian Province (see the diagram) forms a very compact whole, whereas the Andean and the Patagono-Andean Provinces show lower affinities between the areas inside either of them.

1. Guyano-Brazilian Province

This province combines 12 working areal units, presenting various geobotanical formations. They are all tropical and subtropical, chiefly damp forests, savannas and pampas.

The province comprises 4 areas, the Mexican, the Central American, the Amazonian and the Brazil-Uruguay. The first two areas constitute a kind of termination of the transitional zone between the Holarctic and Neotropical Regions. Beyond these areas one encounters almost exclusively Neotropical species (*Felis concolor* and *Mustela frenata* are exceptions). The composition of the fauna of this province is given in Fig. 25.

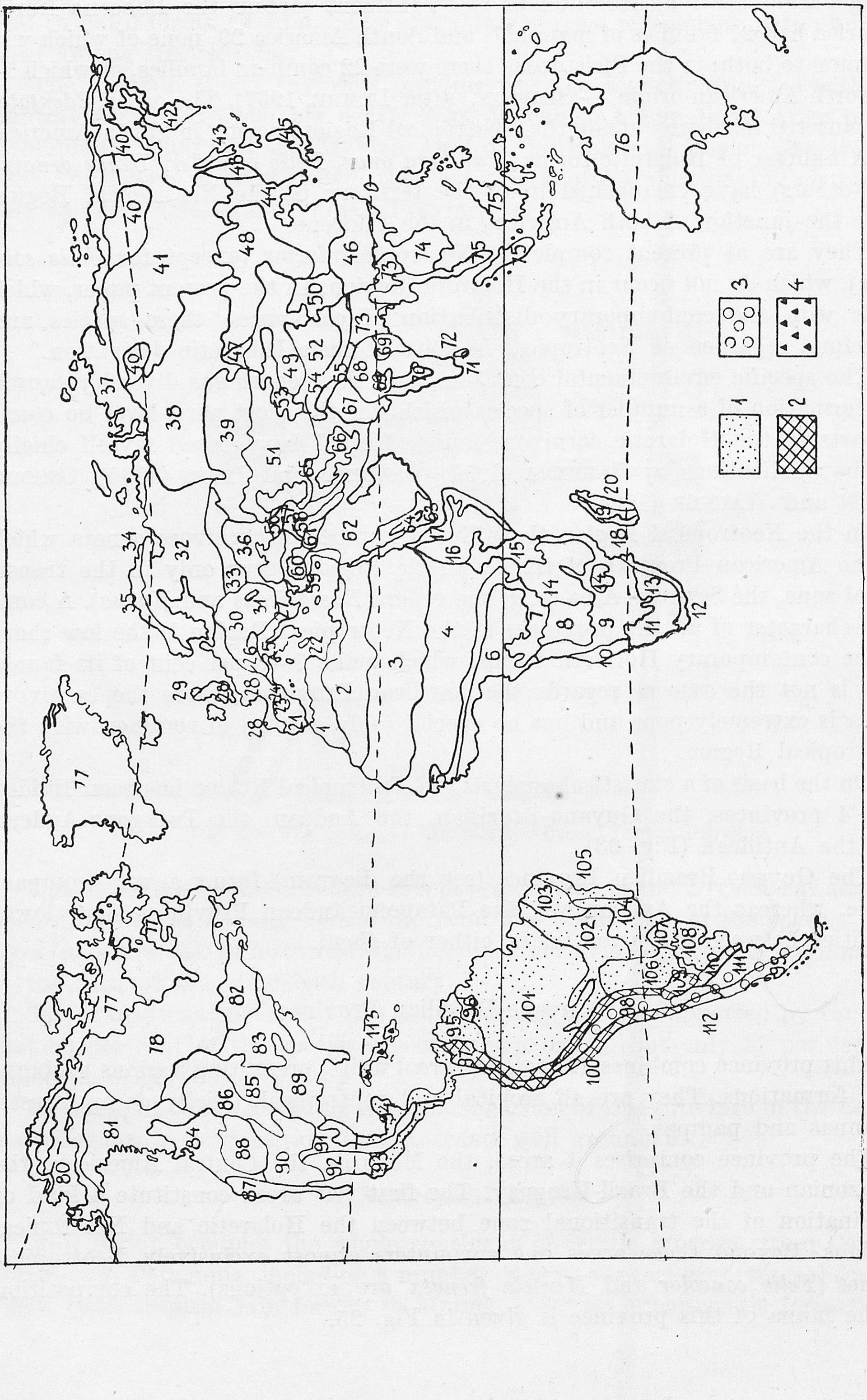


Fig. 23. Provinces of the Neotropical Region. 1 — Guyano-Brazilian, 2 — Andean, 3 — Patagono-Andean, 4 — Antillean

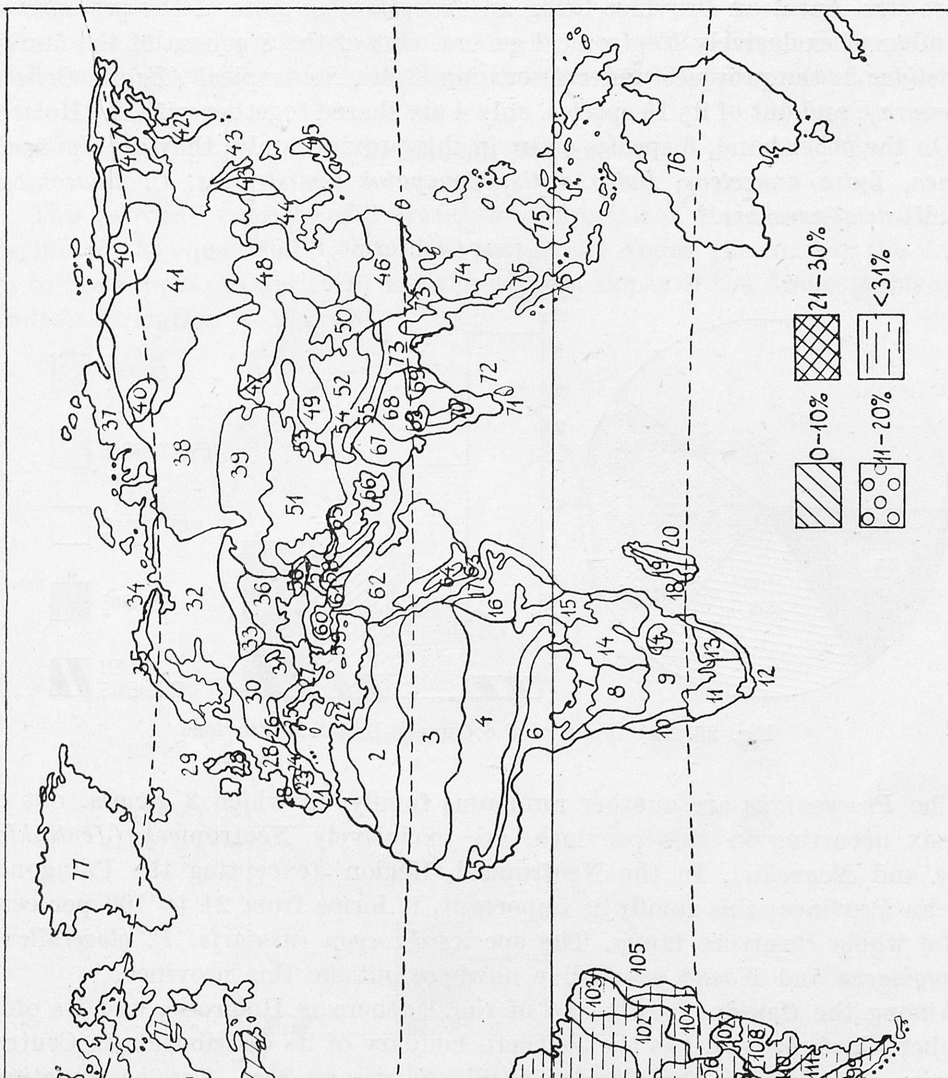


Fig. 24. The share of Neotropical elements

A distinctive feature of the Neotropical faunas is their „musteloidal" nature (the Antillean Province being an exception) in spite of the presence of a number of exclusively Neotropical genera. Out of the 8 genera of the family *Mustelidae* in the province under discussion, 3 are Neotropical (*Tayra*, *Grison*, *Pteronura*), and out of its 19 species, only 4 are shared together with the Holarctic. On the other hand, 6 species occur in this province only; they are *Spilogale pygmea*, *Lutra annectens*, *Lutra mitis*, *Conepatus semistriatus*, *C. amazonicus* and *Mustela paraense*.

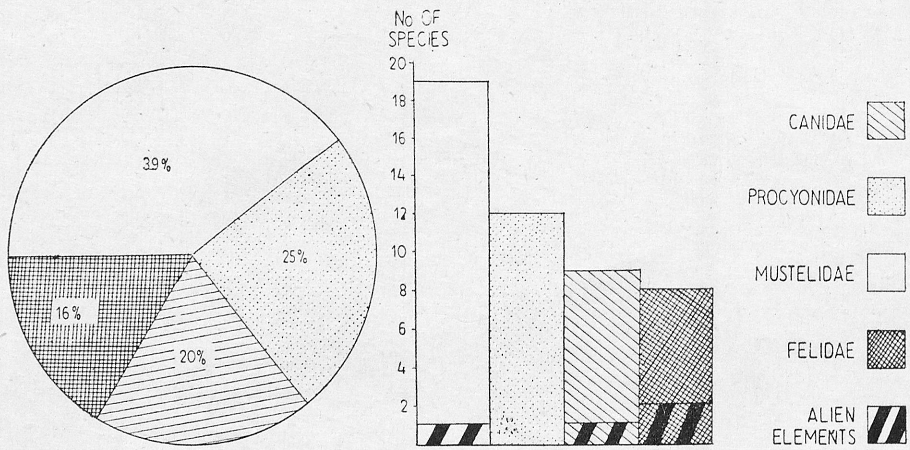


Fig. 25. The fauna of the Guyano-Brazilian Province

The *Procyonidae* are another numerous family, in which 3 genera, out of the six occurring in this province, are exclusively Neotropical (*Jentinkia*, *Potos* and *Nasuella*). In the Neotropical Region (excepting the Patagono-Andean Province) this family is important, it forms from 21 to 100 per cent of the whole carnivore fauna. The species *Procyon insularis*, *P. gloveralleni*, *P. pygmaeus* and *Nasua nasua* live nowhere outside this province.

Among the *Canidae* hardly one of the 7 genera is Holarctic, and its only member, *Canis latrans*, has the southern boudary of its distribution in Central America. In addition, there are two endemic species here, *Speothos venaticus* and *Atelocynus microtis*.

The felid fauna is also abundant and contains 2 Holarctic species, *Felis concolor* and *Lynx rufus*, of which the latter has its southern range in southern Mexico.

The number of endemic species occurring in this province is relatively large, unparalleled in the other provinces. They make 25 per cent of the whole. Two of its genera are endemic, *Speothos* and *Atelocynus*.

The share of foreign elements (8 per cent) is typical of the whole region. In most areas it comes to 4 per cent, because both *Canis latrans* and *Lynx rufus* do not appear outside the Neotropical part of Mexico.

The affinities of this province with the neighbouring ones are as follows:

Mexican Area with Central American and Sonoran Areas — 75—90 per cent, Central American Area with Amazonian Area — 60—75 per cent, Amazonian Area with Brazil-Uruguay Area — 75—90 per cent, Brazil-Uruguay Area with Subtropical Area of the Andean Province — 60—75 per cent.

2. Andean Province

This province consists of 3 areas, the Subtropical, the Subandean and the Pacific, or the equatorial (Columbian) part of the Andes, the coast of the Pacific up to the Tropic of Capricorn, and the western slopes of the Andes (subtropical Andean formation — Fig. 23).

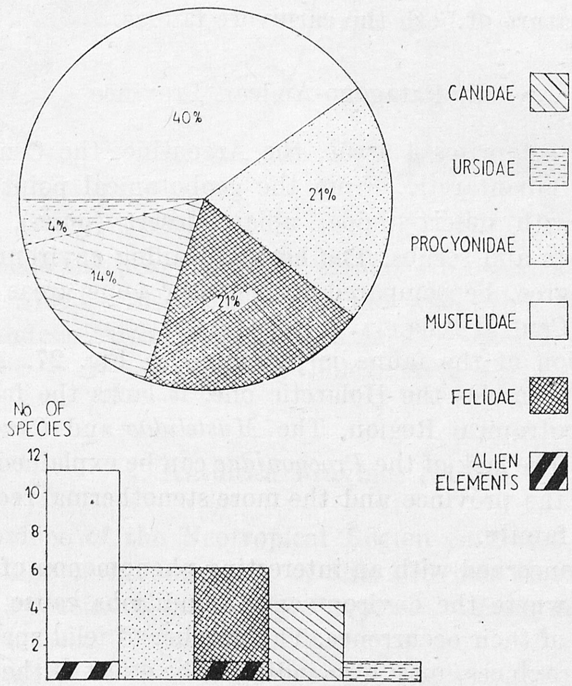


Fig. 26. The fauna of the Andean Province

The province is not very uniform, the two last areas form a kind of joint unit. The carnivore fauna is poorer than that in the previous province. Its composition is given in Fig. 26.

The arrangement of families is somewhat different from that in the Guyano-Brazilian Province, because the *Felidae* take the place of the *Canidae*. This may be explained by the lack of fairly large open areas, which are the most suitable habitat, especially for the Neotropical *Canidae* (see Fig. 27).

In this province lives the only Neotropical member of the *Ursidae*, *Ursus ornatus*, which corresponds to the Oriental species *Ursus malayanus* living in ecologically similar environments. This species occurs only in the Subandean

Area. The Holarctic species *Mustela frenata* and *Felis concolor* also inhabit this province and, as foreign elements, form 8 per cent of the whole carnivore fauna.

Lutra colombiana and *Conepatus quitensis (Mustelidae)* have their ranges confined to this territory only.

The affinities with the areas of the next province, the Patagono-Andean, lie within limits of 50—60 per cent and only those of the Subandean Area with the Central Andean Area of the same province reach 60—75 per cent.

Both the provinces discussed above have some characters in common, which is due to similar ecological conditions. The relatively large share of the *Procyonidae*, which find the most advantageous environmental conditions here, is a distinctive feature of both the carnivore faunas.

3. Patagono-Andean Province

This province comprises 4 areas, the Argentine, the Central Andean, the Chilean and the Subantarctic. From the geobotanical point of view, we are concerned here with desert-steppe, upland-desert (puna), and xerophilous subantarctic forests and scrubs. The here prevailing environmental conditions may, to some degree, be compared to those in some areas of the Holarctic Region, e. g., in Central Asia.

The composition of the fauna is presented in Fig. 27. At first sight the carnivore fauna resembles the Holarctic one, it lacks the family *Procyonidae* typical of the Neotropical Region. The *Mustelidae* and *Canidae* form 88 per cent of the fauna. The lack of the *Procyonidae* can be explained by the markedly cooler climate of the province and the more stenothermal requirements of the members of this family.

Here we are concerned with an interesting phenomenon of bipolarity of the carnivore faunas where the environmental conditions cause the formation of a definite scheme of their occurrence. The number of felid species, smaller than in the previous provinces, may also indicate the effect of the cooler climate on the composition of the fauna.

The number of foreign elements is the same as in the previous province and they form 6 per cent of the total of carnivore species.

A number of the species which occur here are quite absent from the other provinces, e. g., *Conepatus castaneus*, *C. rex*, *Lutra felina*, *L. provocax*, *Lyncodon patagonicus* (endemic genus), *Grison cuja (Mustelidae)*; *Dusicyon inca*, *D. culpaeus*, *D. gracilis*, *D. fulvipes (Canidae)*; *Felis guigna (Felidae)*.

In connection with the large number of species of the genera *Dusicyon*, *Lutra* and *Conepatus* (the same relates also to the provinces discussed previously) the question arises whether some of these forms are not subspecies only, if they show any taxonomic distinctness at all.

Having no museum specimens at my disposal, I had to base myself on the

faunistic elaborations. The number of these „species“ would perhaps be reduced as a result of a critical survey of the material.

It should be added on this occasion that the species *Dusicyon australis* KERR occurred on the Falkland Is., nearest to this province, up to about 1876, when it had been exterminated completely.

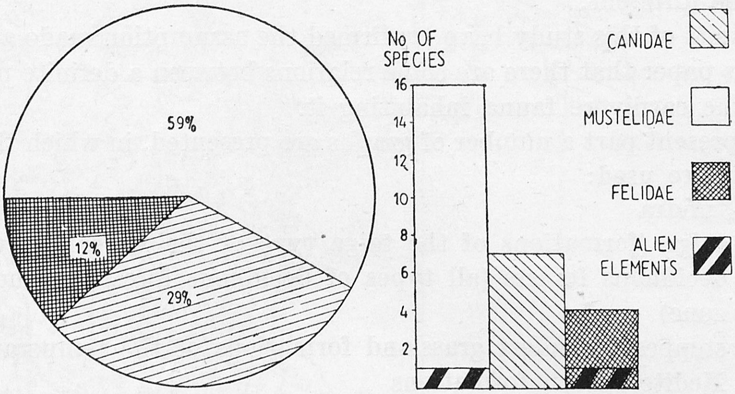


Fig. 27. The fauna of the Patagono-Andean Province

The areas inside the province show various affinities: Argentine Area with Central Andean Area — 75—90 per cent and with other areas — 40—50 per cent; Central Andean Area with Chilean Area — 50—60 per cent and with Subantarctic Area — 40—50 per cent; Chilean Area with Subantarctic Area — 60—75 per cent.

4. Antillean Province (113)

The last province of the Neotropical Region embraces the islands of the Caribbean Sea. The carnivore fauna of this province is extremely poor and consists of only 3 species of the family *Procyonidae*: *Procyon maynardii*, *P. minor* and *Nasua nelsoni*.

All these members of the *Procyonidae* are endemic species and their counterparts (the same genera) occur in the South American continent.

As in the previous case, I cannot express my opinion whether they are true species or only subspecific forms. However, this province is part and parcel of the Neotropical Region. As it has no species in common with the other provinces of the Neotropical Region, it shows no affinities with them in the diagram.

IV. CONCLUSIONS

Owing to the application of 2 independent statistical methods, the dendritic and that of CZEKANOWSKI's diagram I managed to obtain results which allow the zoogeographical regionalization of the world on the basis of affinities of the carnivore fauna.

These results are fully comparable and, virtually, provide identical pictures. The problem of comparison of the results based on the distribution of members of one mammalian order with those obtained by the same methods but using another mammalian order or another group of animals remains open. It might be presupposed that the findings collected during such investigations would probably be different.

The results of this study have confirmed the assumption made at the beginning of this paper that there are some relations between a definite plant formation and the carnivore fauna inhabiting it.

In the present part a number of graphs are presented, in which the following denotations are used:

TD — tundra
TG — taiga (formations of the taiga type of the Boreal Province)
DF — deciduous forests (all types of deciduous forests of the temperate zone)
ST — steppes (woodless grassland formations of the temperate zone)
ME — Mediterranean formations
DC — cold deserts in Asia and both Americas
DW — hot deserts of the tropical zone
SA — sawanna (woodless grassland formations of the tropical zone)
TF — tropical forests (all types of forests of the tropical and subtropical zones)
AM — amphibious species (associated with water environment)

Since many species occur in different biomes, their number in particular graphs is higher than the actual number of species of the given family. The graphs show the picture of distribution of the family being discussed.

The same denotations are also used in the list of contemporary carnivores, presented at the end of this paper.

A. Occurrence of Carnivore Families

In this paper I am concerned with all the 7 families of the *Carnivora*, whose number of species and importance in particular provinces and areas are various.
We may, in general, speak about faunas of the „musteloidal“ and „viverroidal“ types, because these two families have the largest numbers of species and give a definite character to particular faunas.

Canidae

This family is relatively numerous; it comprises 36 species distributed in all the continents (in Australia *Canis dingo* brought there by man). The distribution of the *Canidae* is given on Fig. 28, which shows that they are lacking only in Madagascar, the Antilles and the Congolese Province.

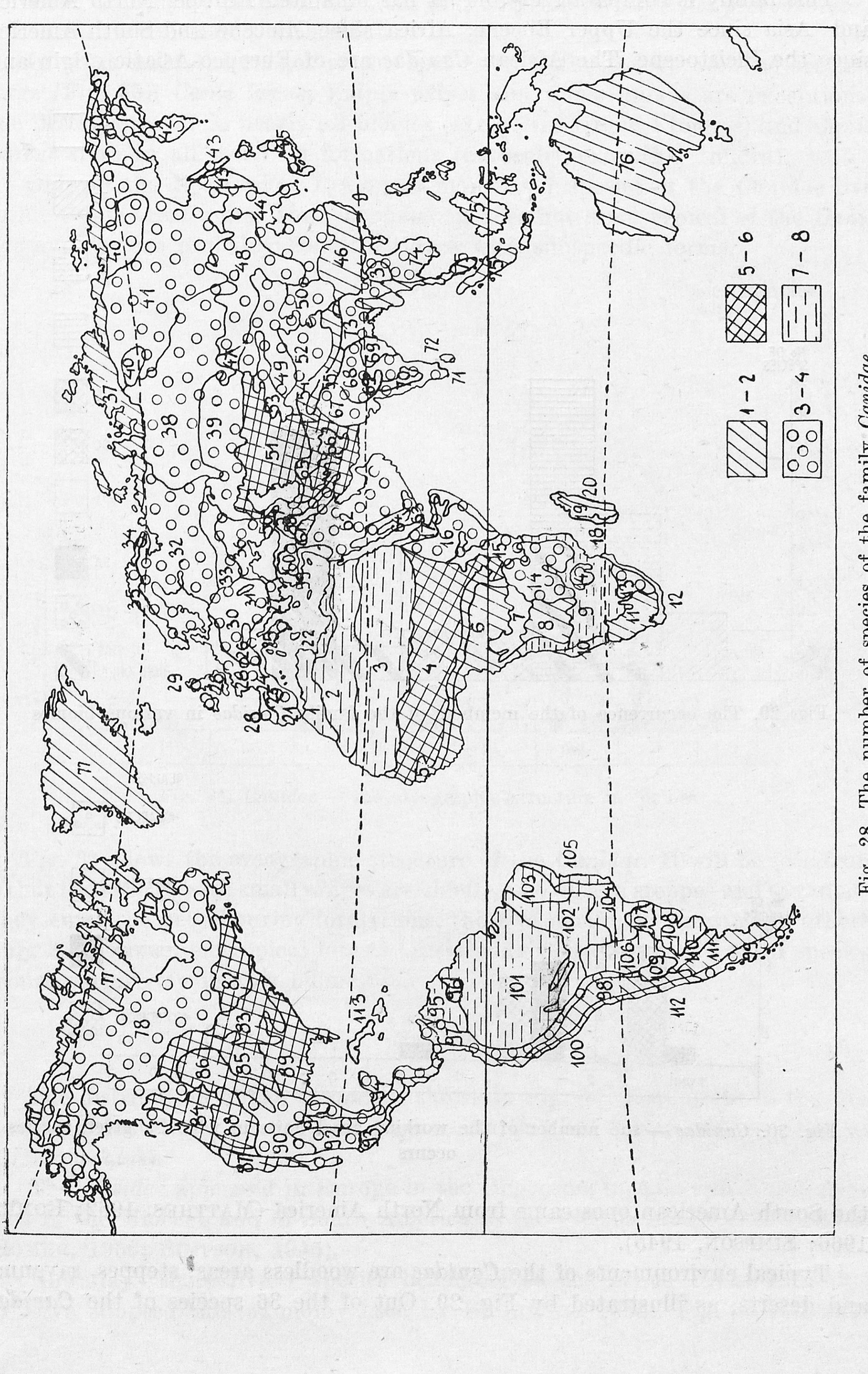


Fig. 28. The number of species of the family *Canidae*

This family is comparatively old; it has inhabited Europe, North America and Asia since the Upper Eocene, Africa since Miocene and South America since the Pleistocene. The African *Canidae* are of Europeo-Asiatic origin and

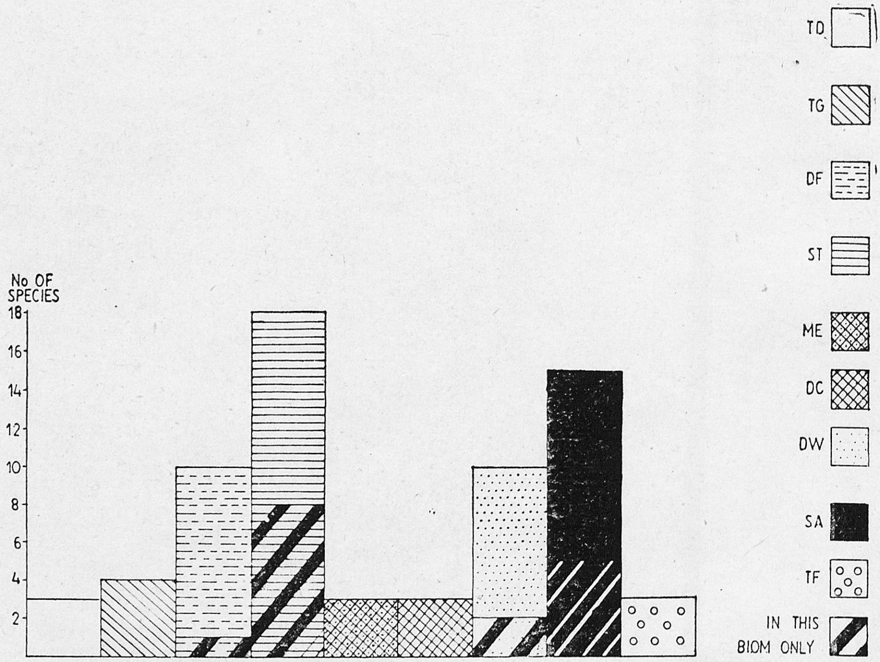


Fig. 29. The occurrence of the members of the family *Canidae* in various biomes

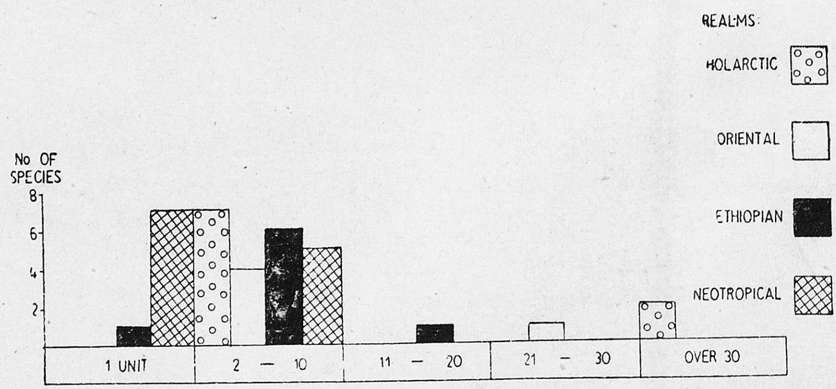


Fig. 30. *Canidae* — the number of the working areal units in which a given species occurs

the South American ones came from North America (Matthes, 1962; Romer, 1966; Simpson, 1945).

Typical environments of the *Canidae* are woodless areas: steppes, savannas and deserts, as illustrated by Fig. 29. Out of the 36 species of the *Canidae*,

15 occur exclusively in woodless areas and only one (*Nyctereutes procyonoides*) is constantly associated with forests.

In most cases the ranges of the species from the family *Canidae* are not large (Fig. 30). *Canis lupus*, *Vulpes vulpes* and *Canis aureus* are exceptions; the first two occur in nearly all biomes (except for tropical forests) and *Canis aureus* lives in all woodless formations (naturally excepting tundra).

Only in the Neotropical Region as many as 7 species of the *Canidae* live inside single areal units. This phenomenon does not seem typical of the *Canidae* and we are probably concerned here with subspecific forms.

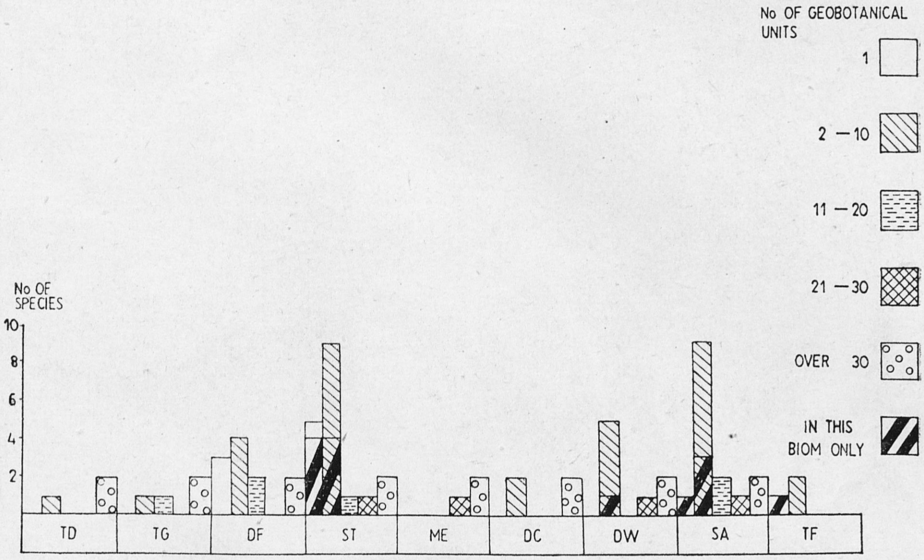


Fig. 31. *Canidae* — the areographic structure in biomes

Fig. 31 shows the areographic structure of the *Canidae*. It will be seen from it that the species with small ranges are chiefly met with in steppes and savannas. They enter the neighbouring formations, those of deciduous forests and others. Only 2 species enter tropical forests (*Atelocynus microtis*, being a third species, occurs exclusively in this biome).

Ursidae

The distribution of the *Ursidae* is shown in Fig. 32. They occur in the Holarctic, Oriental and Neotropical Regions (in this last region only one species, *Ursus ornatus*).

The *Ursidae* appeared in Europe in the Oligocene, in Asia and North America in the Miocene and in South America in the Pleistocene (Matthes, 1962; Romer, 1966; Simpson, 1945).

Nowadays there live 7 species belonging to the genus *Ursus* Linnaeus (I have adopted the taxonomy used by Erdbrink, 1953). Fig. 33 illustrates

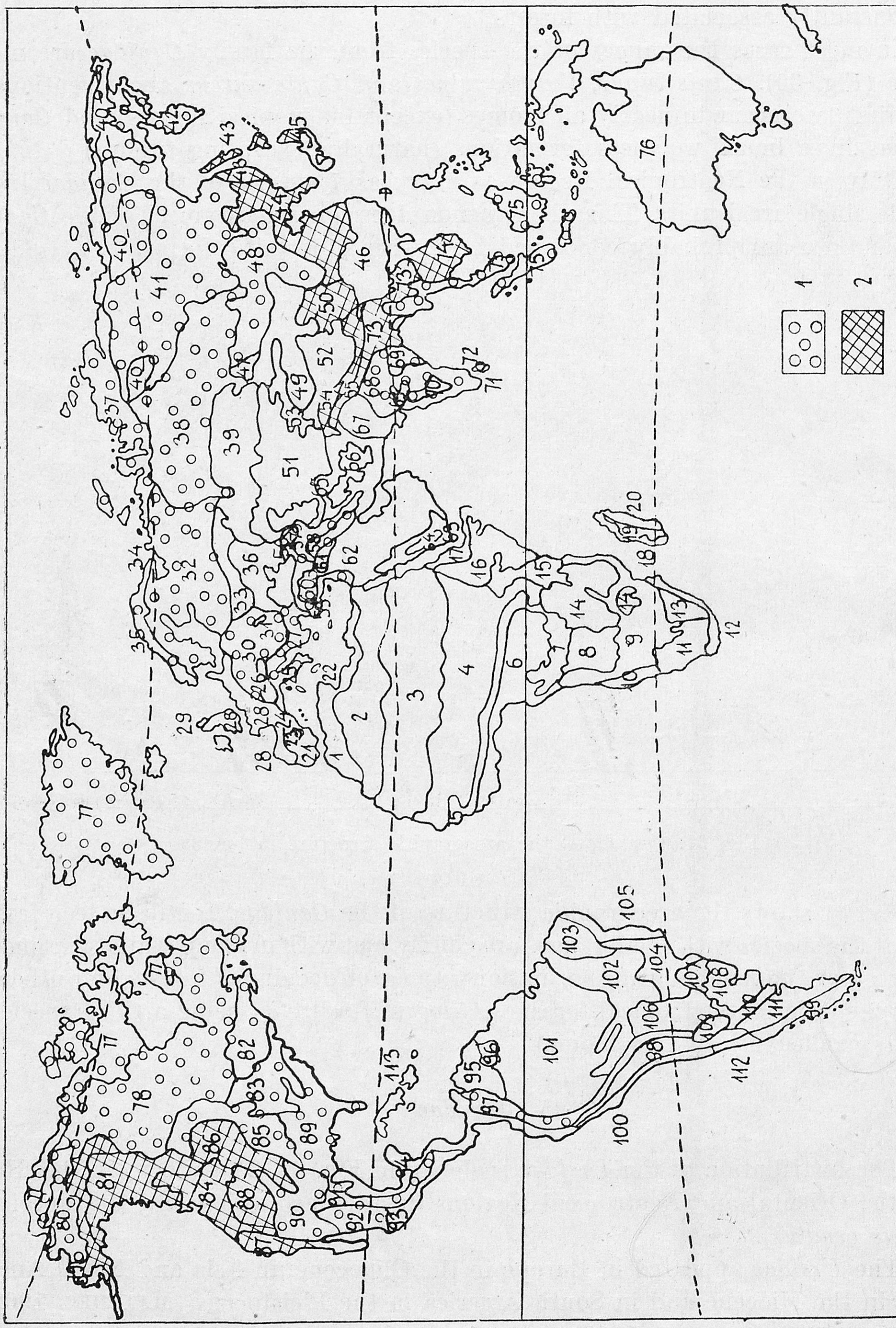


Fig. 32. The number of species of the famila *Ursidae*

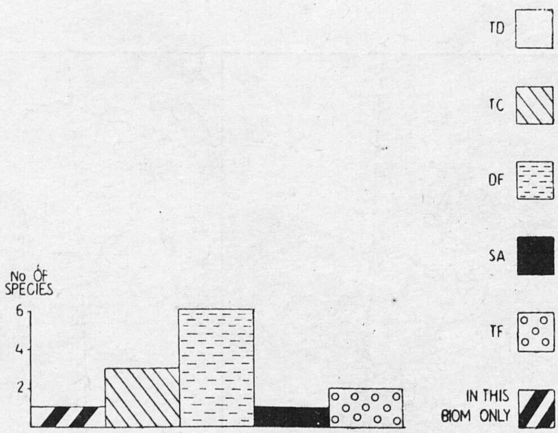


Fig. 33. The occurrence of the members of the family *Ursidae* in various biomes

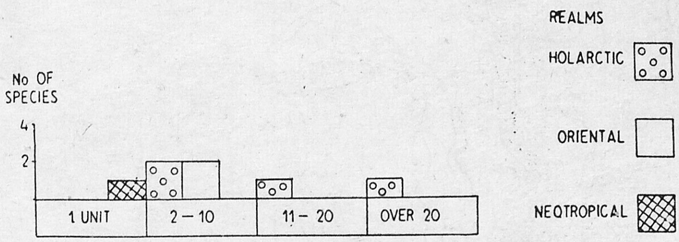


Fig. 34. *Ursidae* — the number of the working areal units in which a given species occurs

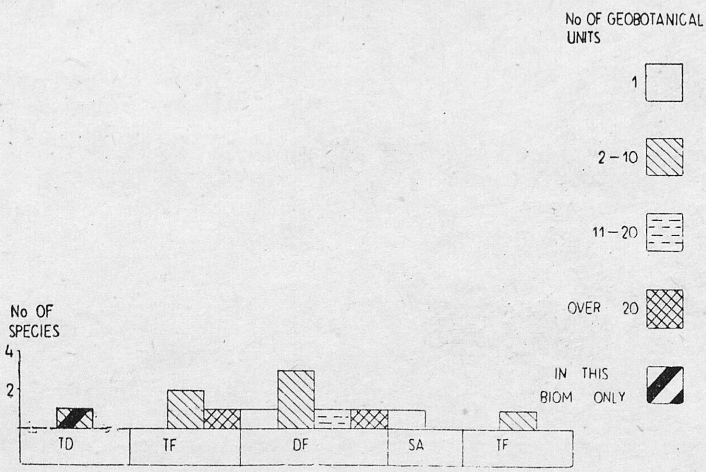


Fig. 35. *Ursidae* — the areographic structure in biomes

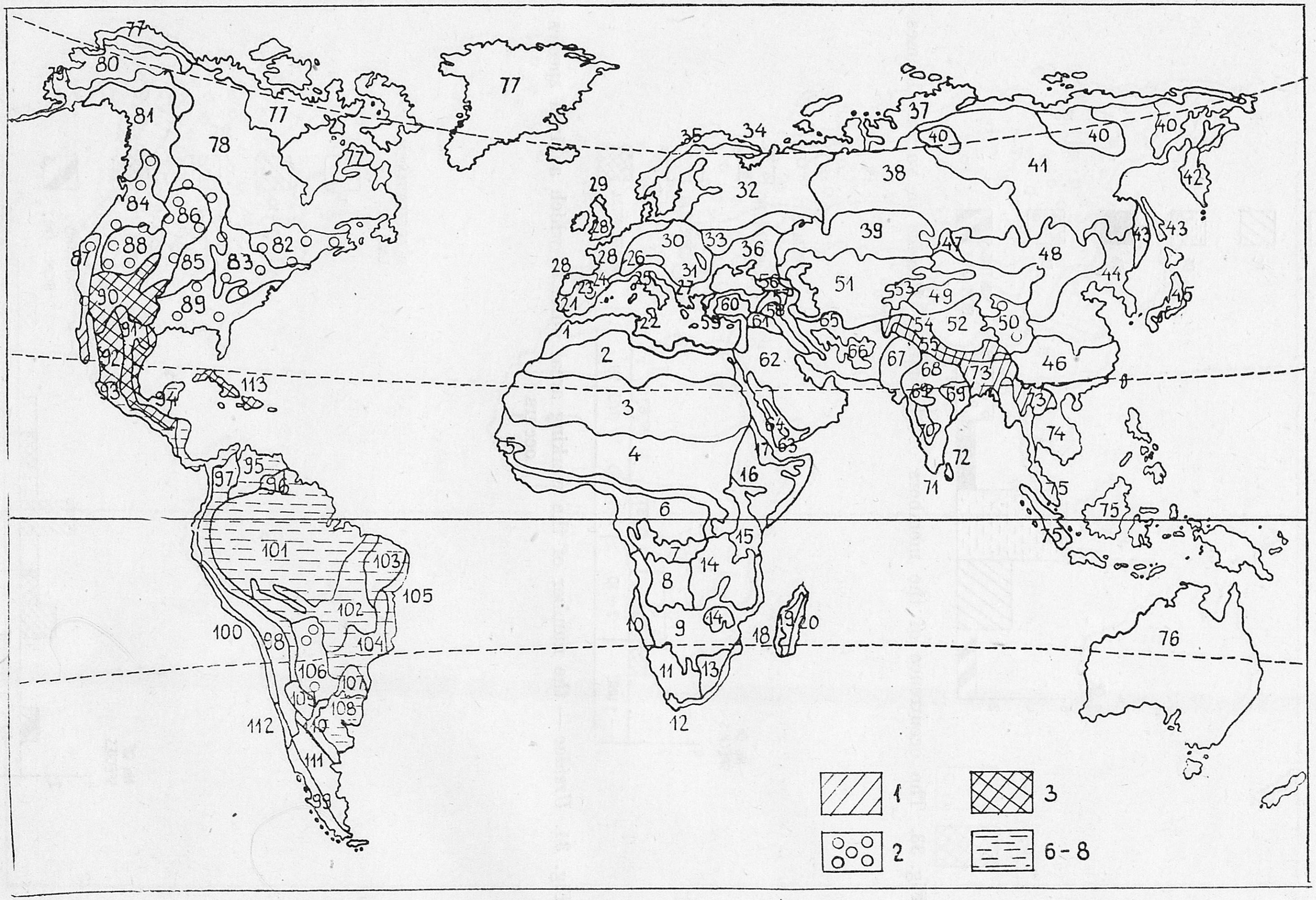


Fig. 36. The number of species of the family *Procyonidae*

the occurrence of the *Ursidae* in various biomes. Forest environments predominate with the exception of *Ursus maritimus*, which occurs circumpolarly in the arctic tundra of the continent and islands of the Arctic Ocean and on the coastal ice.

The Neotropical species, *Ursus ornatus*, is, in addition, encountered in savannas. The Oriental species, *Ursus malayanus* and *Ursus ursinus*, occur in tropical forests.

Most species of the *Ursidae* have small ranges, covering 2—10 working areal units, and *Ursus ornatus* inhabits only one unit. *Ursus arctos* has the most extensive range, from Europe up to North America. Fig. 35 shows the areographic structure of the *Ursidae*.

Procyonidae

The family *Procyonidae*, not very numerous at present, is distributed in North and South America and in Asia (Fig. 36). It has been inhabiting North America since the Oligocene, Asia since the Lower Pliocene and South America since the Upper Miocene. The *Procyonidae* lived in Europe from the Lower Oligocene to the Lower Pleistocene (Matthes, 1962; Romer, 1966; Simpson, 1945).

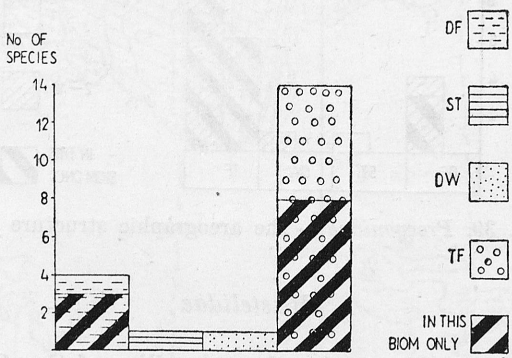


Fig. 37. The occurrence of the members of the family *Procyonidae* in various biomes

The status of the *Procyonidae* in Asia may be regarded as a relict one. Now there live only 2 species there (members of the endemic genera *Ailurus* and *Ailuropoda*). At the present time the *Procyonidae* show the greatest development in the Neotropical Region, where most of the contemporary species occur. They are absent only from the cooler areas of South America.

Fig. 37 presents the ecological characteristics of this family. The species occurring in the biome of tropical forest are absolutely prevalent. The Holarctic species inhabit deciduous forests. Only one species (*Bassariscus astutus*) appears also in woodless rocky environments.

The *Procyonidae* have small ranges, which include less than 10 working areal units (Fig. 38) and even then generally cover only one biome, namely, that of tropical forest (Fig. 39).

Out of the Neotropical genera of the *Procyonidae*, two, *Jentinkia* and *Potos*, are endemic, whereas the three species which live in the Antilles and whose specific autonomy seems dubious present a separate problem (see p. 351).

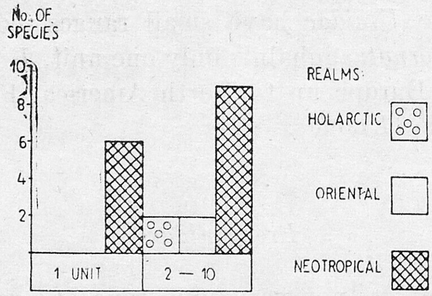


Fig. 38. *Procyonidae* — the number of the working areal units in which a given species occurs

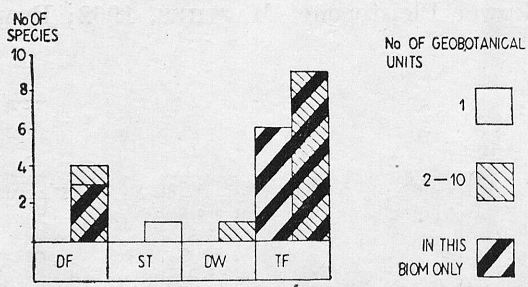


Fig. 39. *Procyonidae* — the areographic structure in biomes

Mustelidae

This is one of the two most abundant families of the *Carnivora* (exceeding the *Viverridae*, which are the other) and its 74 species occur in all the continents except Australia. Fig. 40 shows that they are the most numerous in the Holarctic (Europe and East Asia), South-East Asia (Oriental Region) and South America.

The *Mustelidae* appeared in Europe in the Eocene, in North America and Asia in the Oligocene, in Africa in the Middle Pliocene and in South America in the Upper Pliocene (Matthes, 1962; Romer, 1966; Simpson, 1945).

This is the only carnivore family that lives in all the biomes specified in this paper, from tundra to tropical forest (Fig. 41). It will be seen from Fig. 41 that a large number of species are associated with water environment and have amphibious ways of living. Such species form 80 per cent of the 20 species of the *Mustelidae* inhabiting tropical forests.

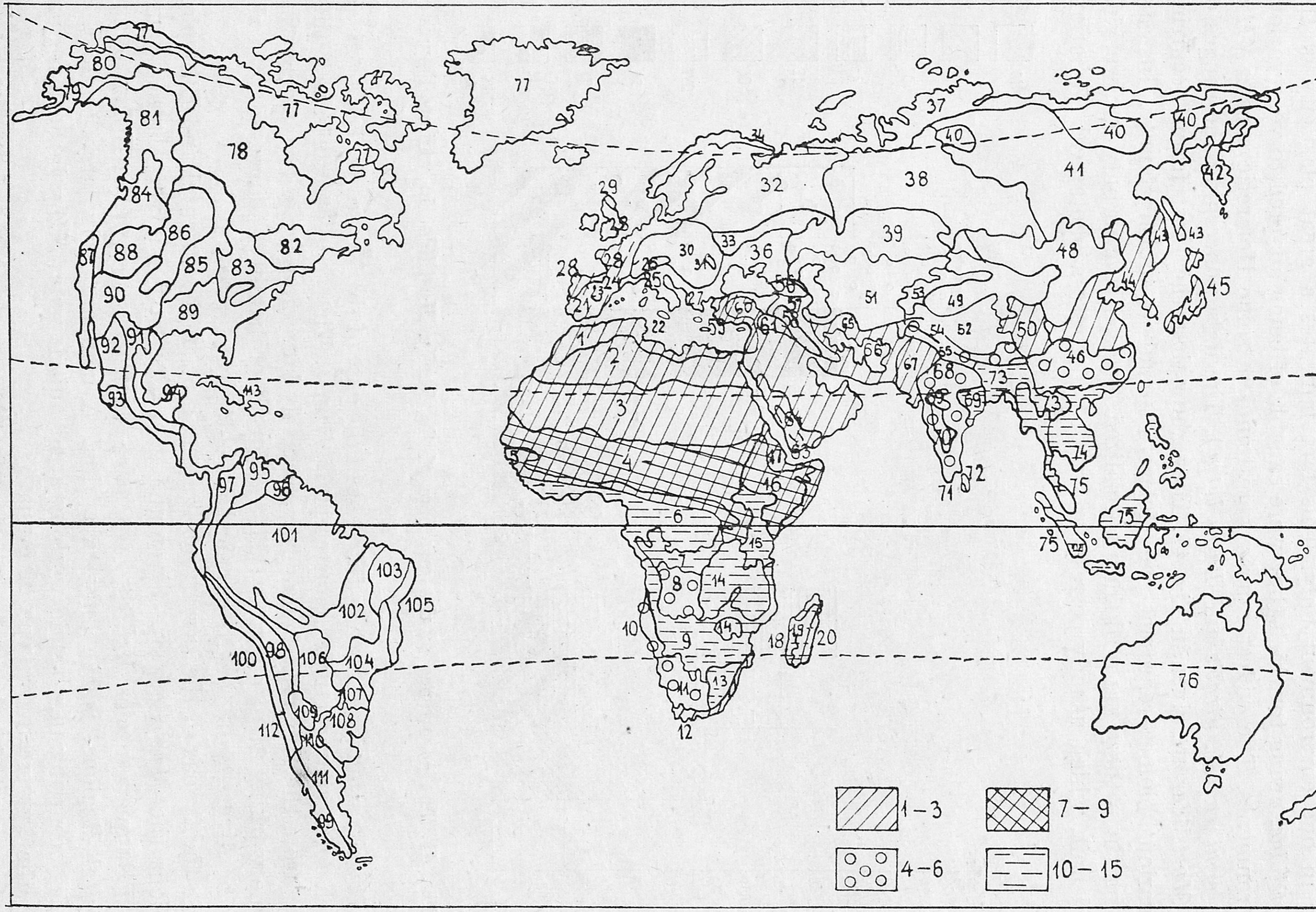


Fig. 40. The number of species of the family *Mustelidae*

The remaining biomes are characterized by a low percentage of forms living in one environment only. This fact indicates a great plasticity of the *Mustelidae*, owing to which they were capable of being adapted to very various environments. The widest ranges were found in some Holarctic species *(Mustela erminea, M. nivalis* and *Lutra lutra)*. The data concerning the ranges of the *Mustelidae* are given in Fig. 42. They show that the most forms occurring in various biomes represent the Holarctic members of this family. Instead, among them there are no highly specialized forms, living in only one working areal unit, which usually corresponds with a definite geobotanical formation.

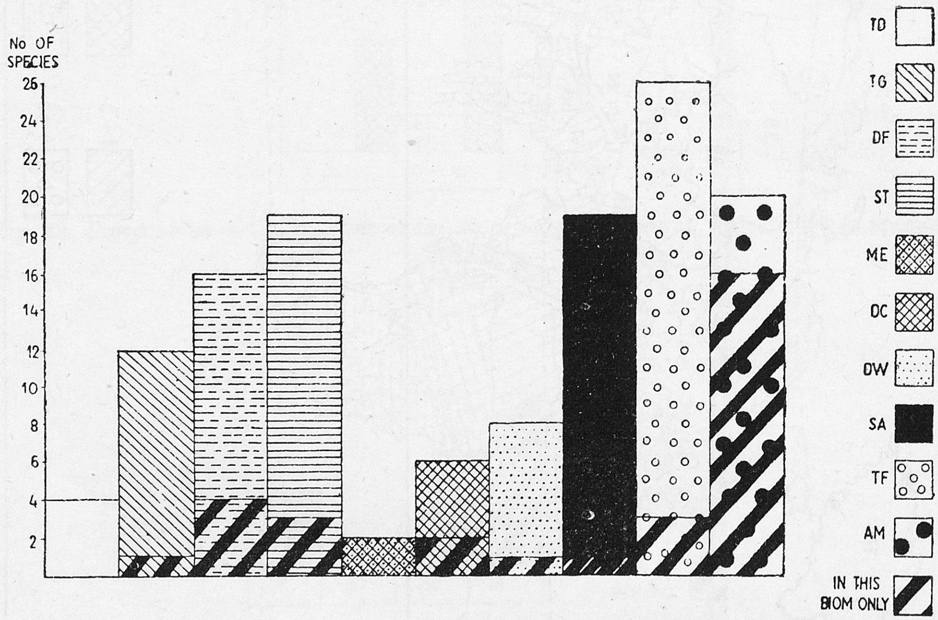


Fig. 41. The occurrence of the members of the family *Mustelidae* in various biomes

The situation is somewhat different in the case of the Neotropical *Mustelidae*, which form characteristic „musteloidal" faunas. The character in which they differ from the Holarctic faunas is a relatively large number of forms occurring in one working areal unit only. This is, in all probability, connected with the specific diversity of the Neotropical geobotanical formations.

In the faunas of the „viverroidal" type, i. e., in the Oriental and Ethiopian Regions the *Mustelidae* are fewer and generally have not very large ranges. The Ethiopian species *Mellivora capensis*, which lives also in the Holarctic and Oriental Regions, is the only exception. A comparatively large number of species occurring in a single working areal unit is noteworthy in both regions with the „viverroidal" type of fauna.

The areographical structure of the *Mustelidae* is presented in Fig. 43, which shows that only in the biome of deciduous forest there occur members of the *Mustelidae* belonging to all the range groups. On the other hand, in the zone

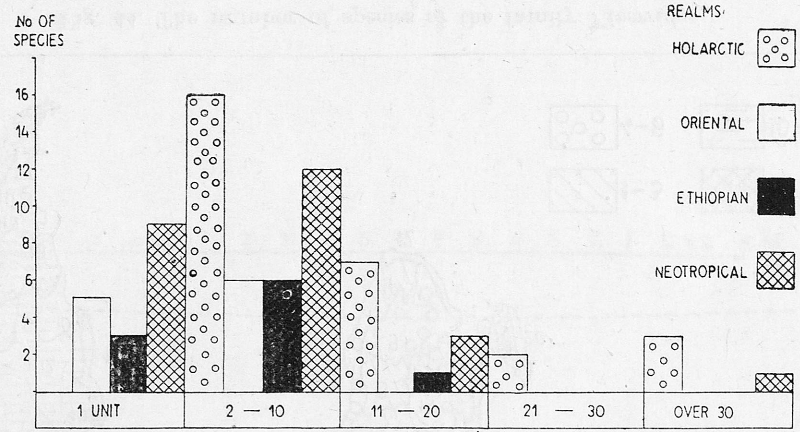


Fig. 42. *Mustelidae* — the number of the working areal units in which a given species occurs

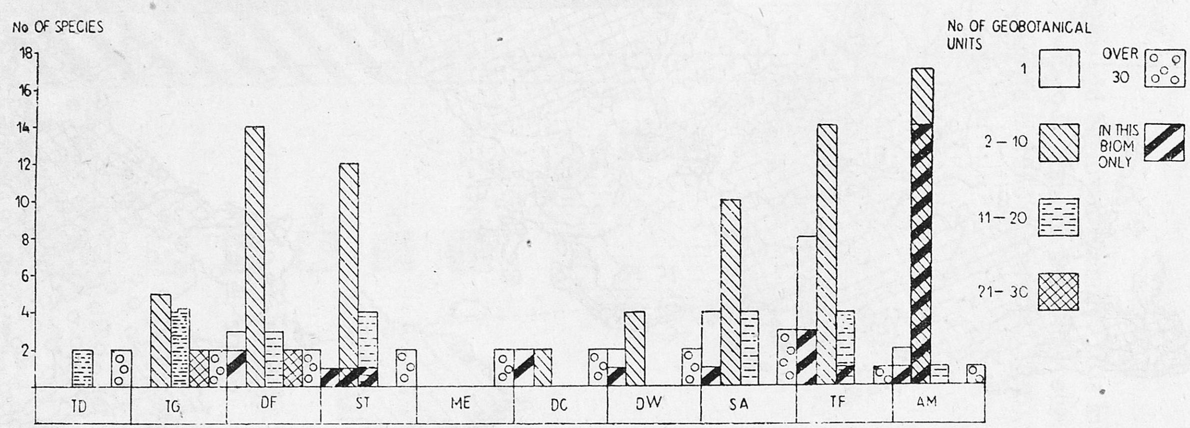


Fig. 43. *Mustelidae* — the areographic structure in biomes

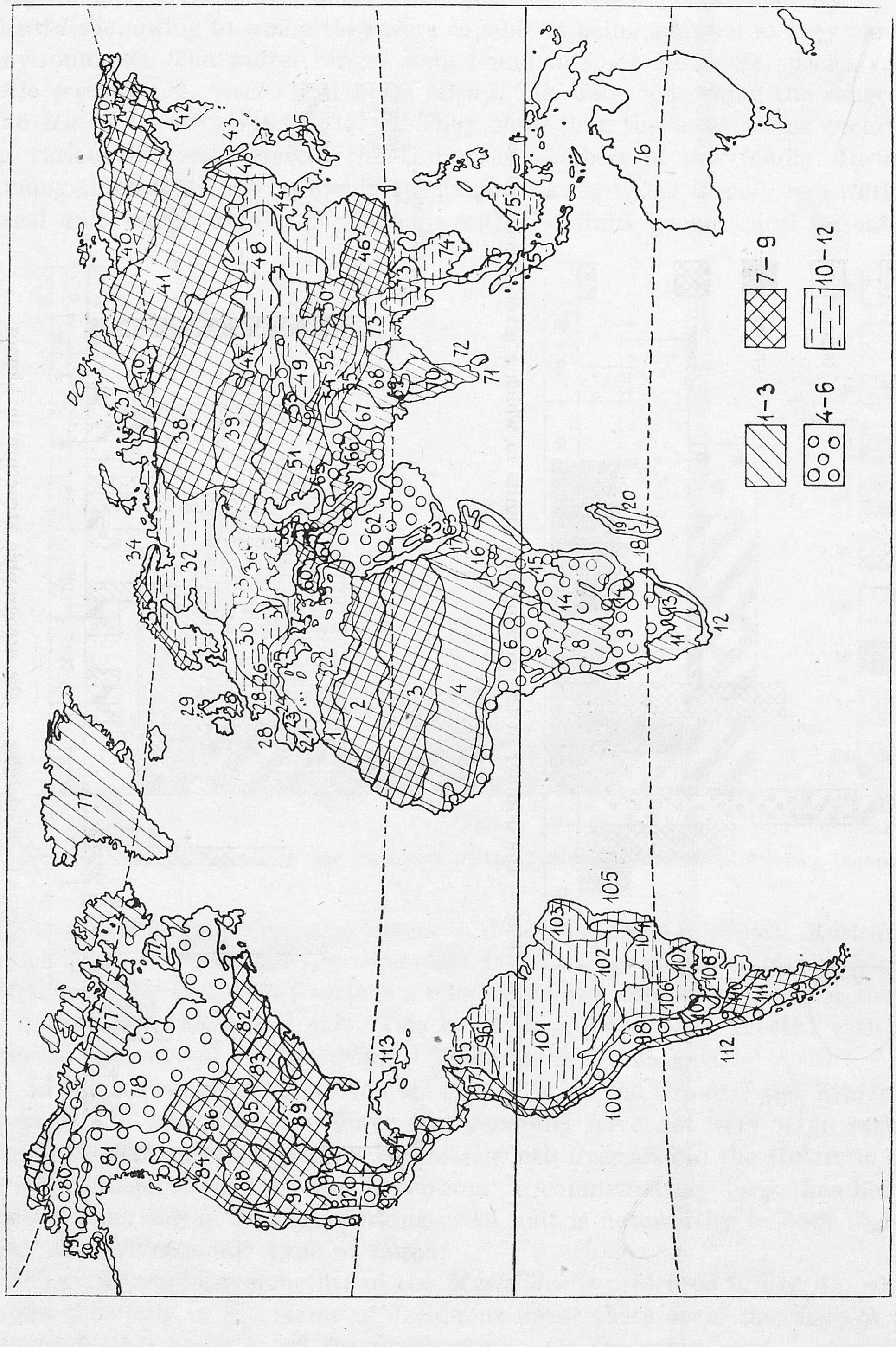


Fig. 44. The number of species of the family *Viverridae*

of Mediterranean vegetation there are only species with the most extensive ranges.

The most numerous species occurring in only one biome are amphibious forms.

Viverridae

This is the second most numerous and also old carnivore family. It is known to have occurred in Europe in the Upper Eocene, in Asia in the Oligocene, and in Africa in the Miocene (MATTHES, 1962; ROMER, 1966; SIMPSON, 1945). The

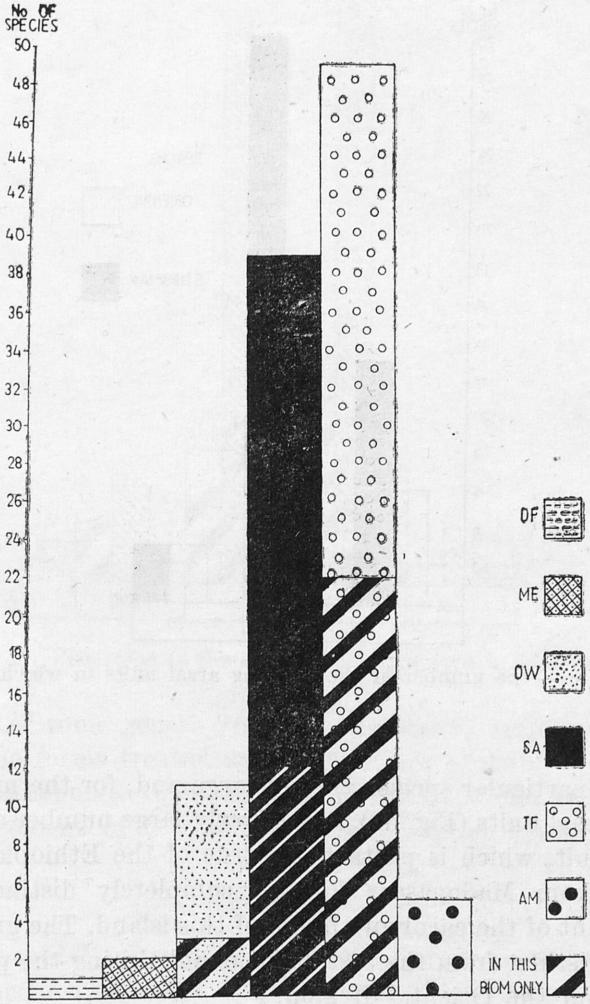


Fig. 45. The occurence of the members of the family *Viverridae* in various biomes

present distribution of the *Viverridae* is illustrated in Fig. 44. They are represented in the largest numbers south of the Sahara in Africa and in South-East Asia. The *Viverridae* encroach in small numbers on the Holarctic provinces

adjacent to the Ethiopian and Oriental Regions, where they are represented by only a few species which have ranges in their native regions. The *Viverridae* are quite clearly well specialized for life under tropical conditions, as indicated by the data from Fig. 45. They occur most numerously in the biomes of savanna and tropical forest and a great many of them do not go beyond these biomes at all. They are also relatively numerous (more numerous than the *Mustelidae*) in the biome of hot deserts. Only a few species are associated with the amphibious ways of living as well as with the biomes of Mediterranean vegetation and deciduous forests.

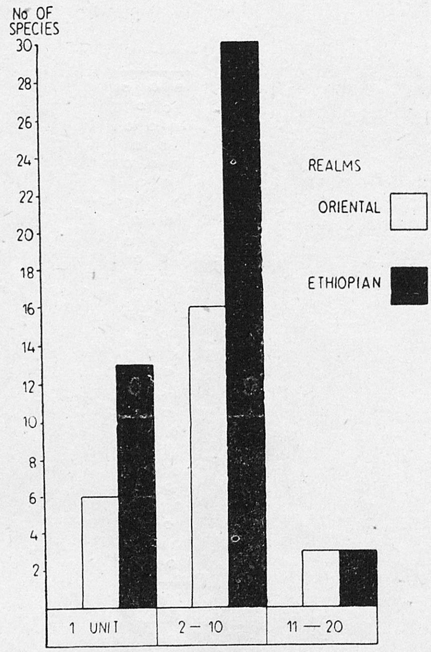


Fig. 46. *Viverridae* — the number of the working areal units in which a given species occurs

The range of particular species are not large and, for the most part, occupy 2—10 working areal units (Fig. 46). A relatively large number of species inhabit only one areal unit, which is particularly true of the Ethiopian forms.

The *Viverridae* from Madagascar form a completely distinct group, which makes 100 per cent of the carnivore fauna of this island. The group of Malagasy species is quite distinct from the rest of forms inhabiting the provinces of both the Ethiopian and the Oriental Region.

In the Ethiopian and Oriental Regions the *Viverridae* give the there existing carnivore faunas their „viverroidal“ character.

The areographic structure of the *Viverridae* is shown in Fig. 47. It supports the opinion that only the species which are widely distributed inside the regions

go beyond their boundaries into some biomes in other regions (e. g., *Genetta genetta* in Europe). None of the *Viverridae* is permanently associated with the amphibious ways of living. This graph also shows that a relatively large number of viverrid species are specialized for life under specific conditions of savannas and tropical forests. This is evidenced, among other things, by the large number of endemic species and genera, especially the insular ones, in the Oriental Region.

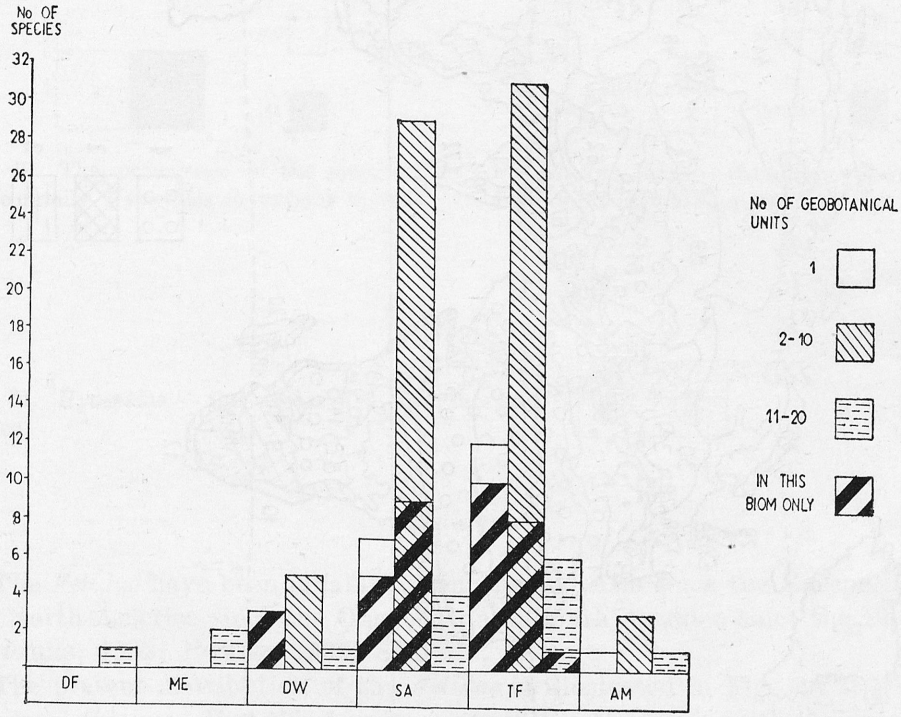


Fig. 47. *Viverridae* — the areographic structure in biomes

The taxonomy of some genera *(Genetta, Herpestes)* seems to be too much expanded and some forms treated as „species" are probably only subspecies. However, even a taxonomic revision of these genera would not influence the areographic arrangement of the family in an essential manner.

Hyaenidae

The family *Hyaenidae* appeared in Asia and Europe in the Miocene and in Africa in the Pliocene (MATTHES, 1962; ROMER, 1966; SIMPSON, 1945). The present distribution of the *Hyaenidae* is shown in Fig. 48. The members of this small family (4 species) occur throughout the Ethiopian Region (except for the Malagasy and Congolese Provinces) and in the savanna-desert biomes of the Holarctic Region.

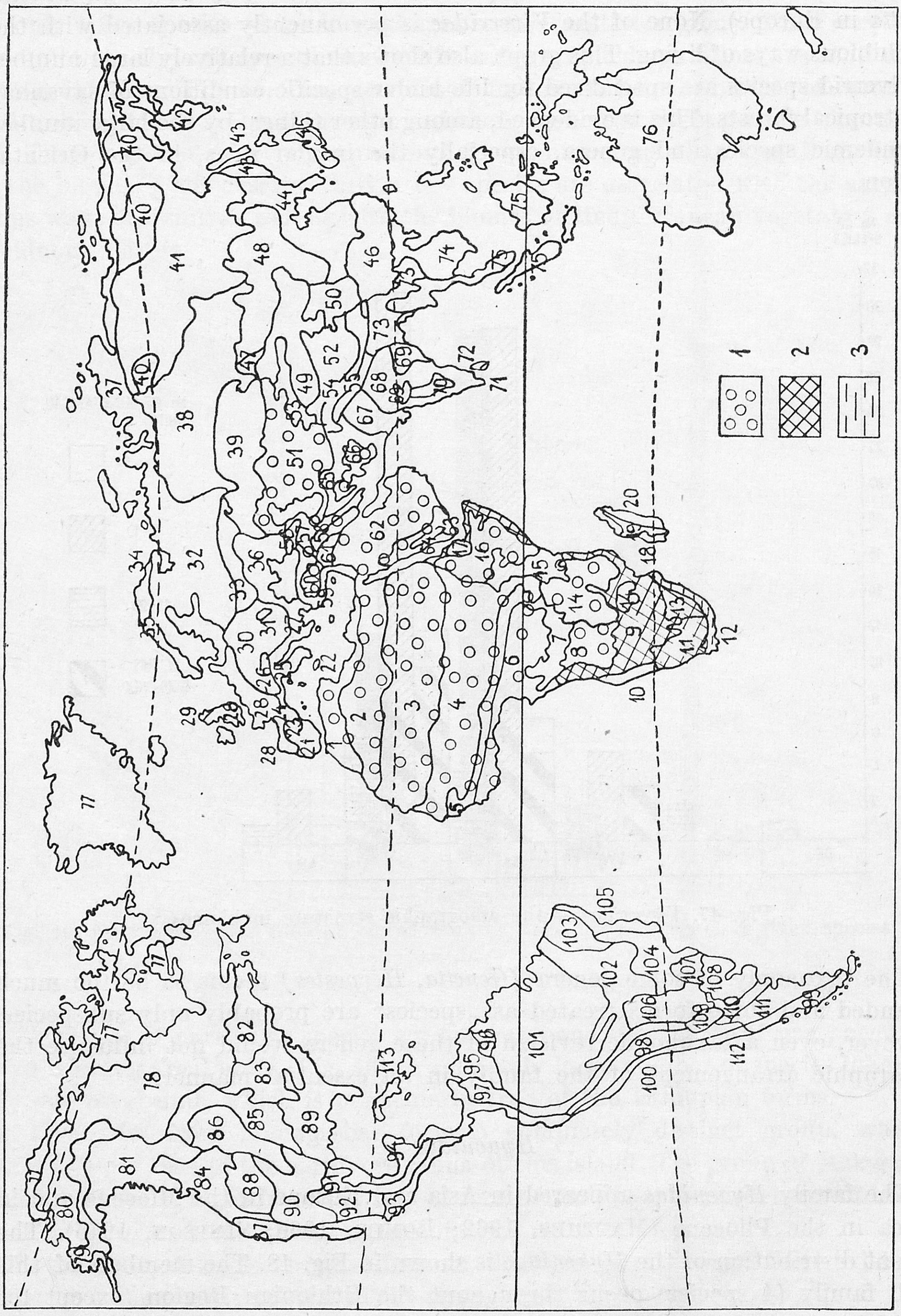


Fig. 48. The number of species of the family *Hyaenidae*

In the Ethiopian Region the *Hyaenidae* are distributed only in the biomes of savanna and desert (Fig. 49). One species *(Hyaena hyaena)* lives both in the Ethiopian and in the Holarctic Region, the other ones only in the Ethiopian Region.

Fig. 51 shows that all the species are uniformly distributed both in the savanna and in the desert.

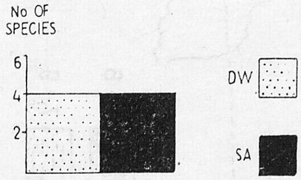


Fig. 49. The occurrence of the members of the family *Hyaenidae* in various biomes

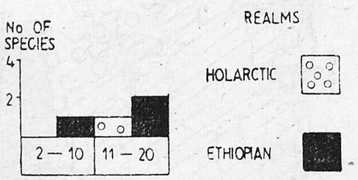


Fig. 50. *Hyaenidae* — the number of working areal units in which a given species occurs

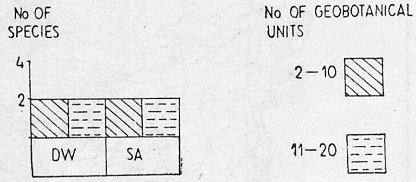


Fig. 51. *Hyaenidae* — the areographic structure in biomes

Felidae

The *Felidae* have been inhabiting Europe and Asia since the Eocene, Africa and North America since the Oligocene, and South America since the Pliocene (Matthes, 1962; Romer, 1966; Simpson, 1945).

The present distribution of the *Felidae* is illustrated in Fig. 52. It will be seen from this map that this family occurs in the Holarctic (with the exception of the tundra biome), Oriental, Ethiopian and Neotropical (except for the Antilles) Regions. The *Felidae* are most numerous in the Oriental Region and in the Guyano-Brazilian Province of the Neotropical Region. They occur in relatively small numbers in the Holarctic Region, especially in its northern part.

Fig. 53 shows that *Felidae* find the optimum living conditions, above all, in the biomes of savannas, tropical forests and hot deserts. A large number of species occur also in the steppe biome. Their great capability to live under various conditions and avoidance of narrow specialization are evidenced by the fact that there is hardly one species (Neotropical *Felis guigna*) that lives in one biome only, that of cold deserts.

The *Felidae* have, as a rule, extensive ranges (Fig. 54), only two species occur exclusively in one geobotanical unit (*Felis minuta* and *Felis badia*, both in the Indonesian-Philippine Area).

Only the Neotropical members of the *Felidae* have somewhat smaller ranges;

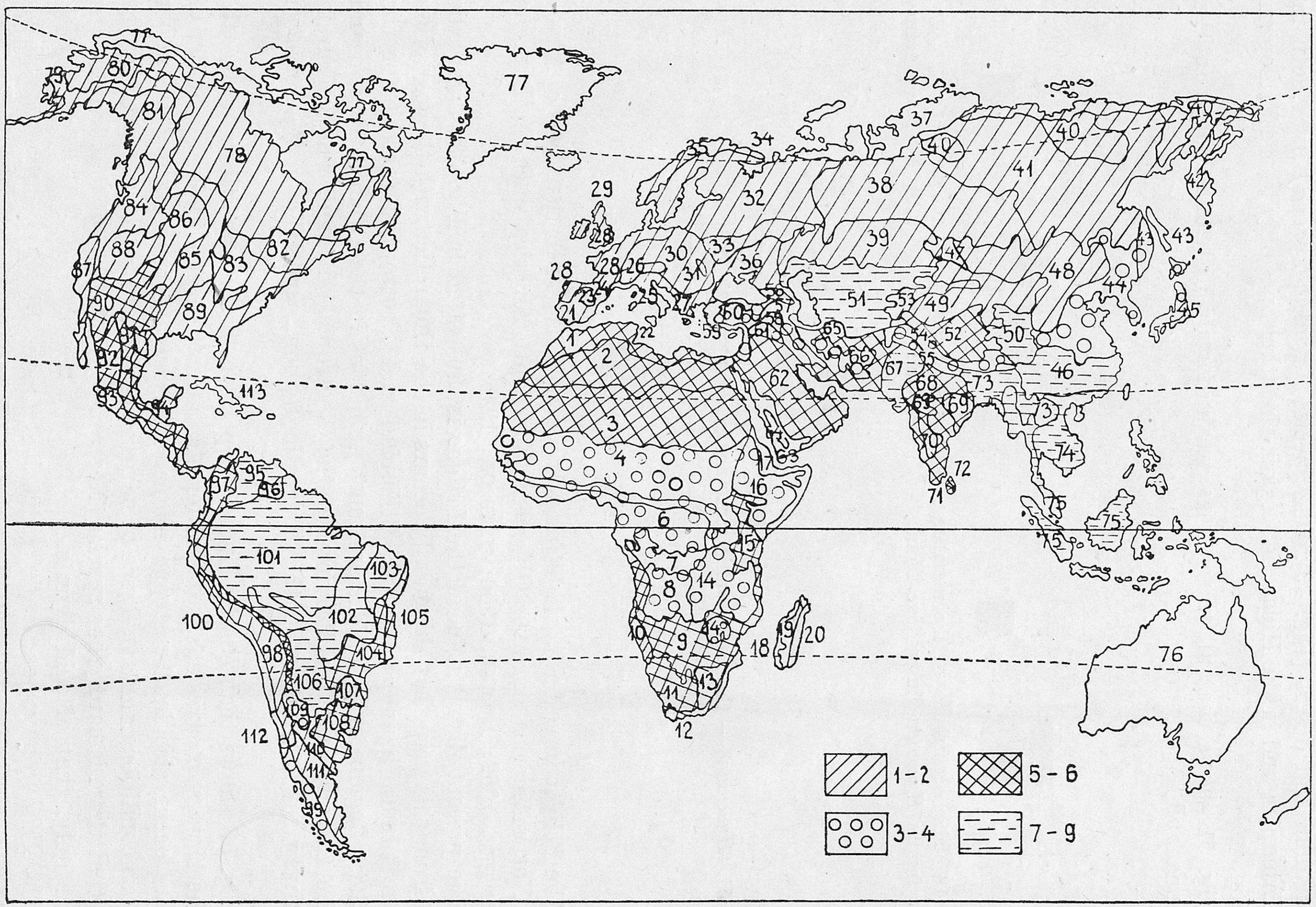


Fig. 52. The number of species of the family *Felidae*

the other species have more or less uniform distribution, that of *Panthera pardus*, which lives in the Oriental, Ethiopian and Holarctic Regions, being the widest.

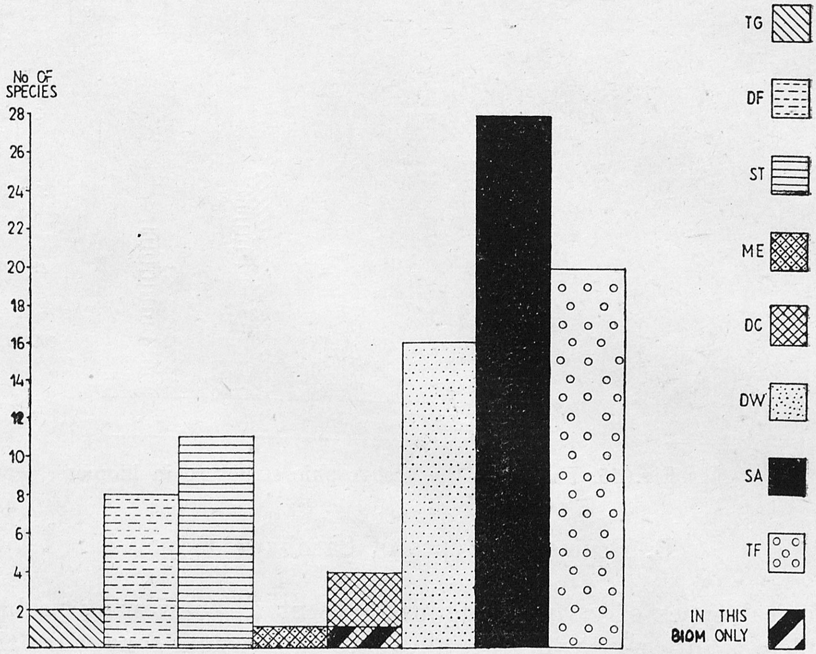


Fig. 53. The occurrence of the members of the family *Felidae* in various biomes

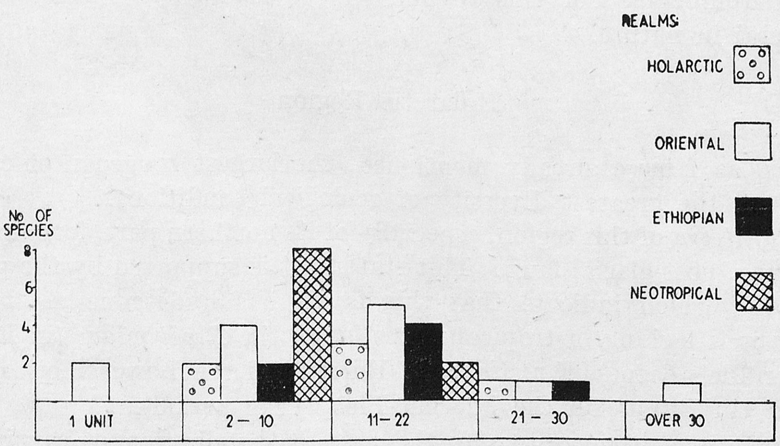


Fig. 54. *Felidae* — the number of the working areal units in which a given species occurs

The areographic structure of the *Felidae* is shown in Fig. 55. A distinctive feature of this structure is the accumulation of most species in the biomes of the tropical zone, where all the types of ranges are observed, from those occu-

pying single areal units to the most extensive ones, the medium-sized ranges being prevalent. The species which occur in the other biomes have medium-sized and small ranges.

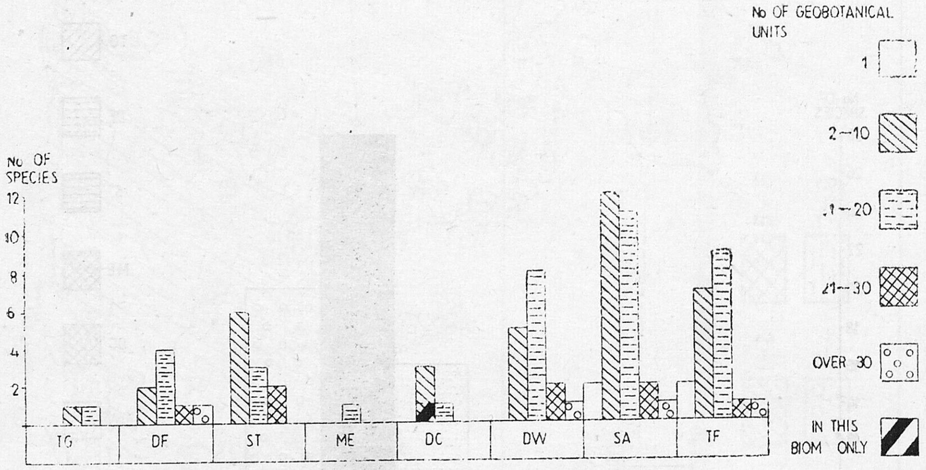


Fig. 55. *Felidae* — the areographic structure in biomes

B. Ecological Types of Carnivore Fauna

Ecological types of carnivore faunas present an interesting problem, but this problem is not easy at all, since adequate publications concerning the whole order are lacking and the biology of some species is poorly known, if known at all. Another difficulty is caused by the fact that many species occur in different environments. For this reason, the considerations offered below are very general in nature.

Holarctic Region

This is, as I have already mentioned, the largest zoogeographical region, which shows the greatest diversity of ecological conditions.

The *Carnivora* of this region, especially of its northern part, form a comparatively young, post-glacial fauna. This statement is supported by the palaeontological data, which indicate that this fauna has undergone great changes; nowadays it is lacking in tropical forms, e. g., the *Procyonidae* (in Europe till the Lower Pleistocene), *Viverridae* (in Europe till the Lower Pleistocene) and *Hyaenidae* (in Europe in the Miocene-Pleistocene period).

This fact is also suggested by the present distribution of carnivores, the lack of endemic species and genera, and the small number of species living in one biome only. The territories unaffected by the glacier at its greatest range, where the refuges of the Tertiary vegetation have been preserved, are an exception. Such territories lie in the borderland between the Holarctic and Oriental Regions.

Fig. 56 shows the distribution of carnivore species in various biomes. Two groups of biomes are distinct here, the forest-steppe group and the desert-savanna one. The latter group occupies the territories on the boundary with the Ethiopian, Oriental and Neotropical Regions. The neighbourhood of these regions exerts a distinct influence on the nature of the there existing fauna, as indicated by the occurrence of members of the *Procyonidae*, *Viverridae*, *Hyaenidae* and some *Felidae* in these territories.

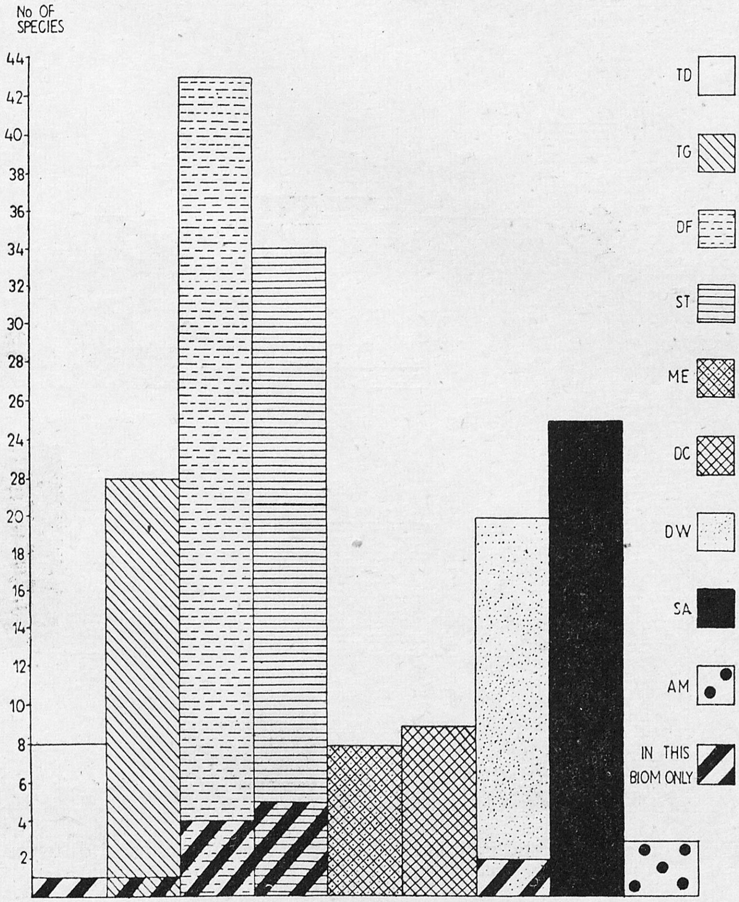


Fig. 56. The ecological type of the carnivore faunas of the Holarctic Region

The basic components of the Holarctic carnivore fauna are the *Mustelidae*' *Canidae* and *Ursidae*. Generally speaking, this fauna is of the „musteloidal" type.

Fig. 57 shows the occurrence of the members of various carnivore families in particular biomes. The diagrams of individual families (*Canidae*, *Mustelidae* and *Felidae*) illustrate a kind of two-peak nature of the distribution of the fauna: the forest-steppe zone and the desert-savanna one. This last zone is especially strongly penetrated by the *Felidae*.

The *Ursidae* represent the inhabitants of the forest zone (naturally with the exception of the tundra-marine form *Ursus maritimus*). The other families *(Viverridae* and *Hyaenidae)* occur marginally in the Holarctic Region.

The *Procyonidae* of the Holarctic are in category by themselves. At the present time this family, which had a far more extensive range in the Miocene and Pliocene (see above), occurs almost exclusively in the Neotropical Region. In the Holarctic a relict station subsists in Southern China and they also occur in the American Province. The *Procyonidae* of the Holarctic remain „silvan" in character.

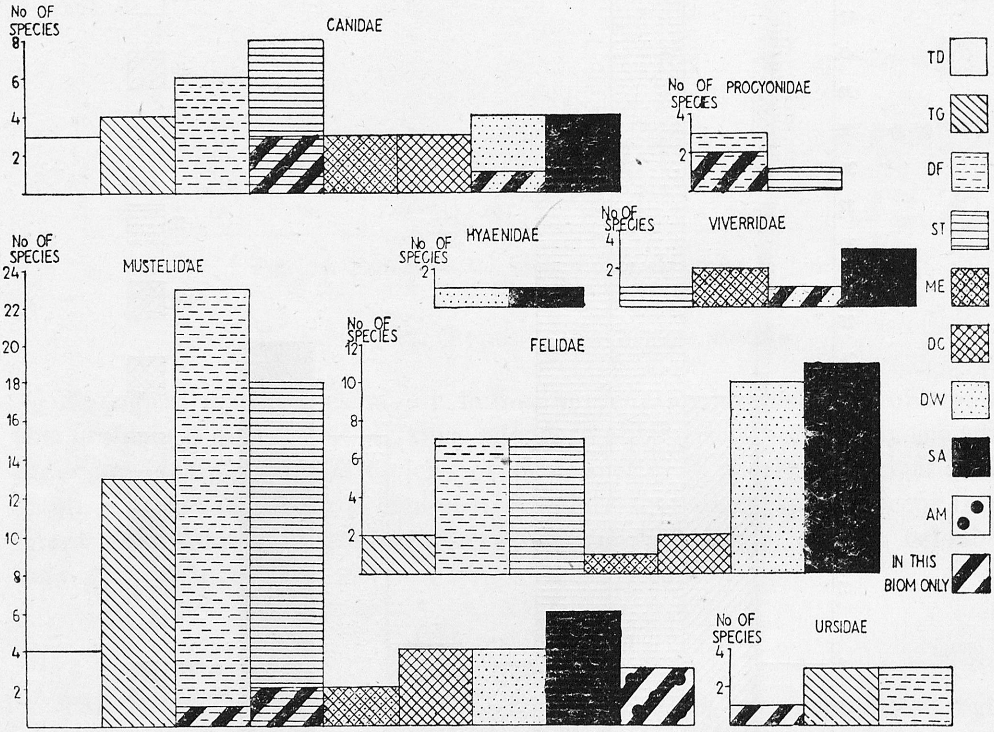


Fig. 57. The occurrence of the members of the carnivore families in different biomes of the Holarctic Region

Oriental Region

The carnivore fauna of the Oriental Region is completely different from that of the Holarctic. It is of the „viverroidal" type and, therefore, the *Viverridae* are represented most numerously. South Asia may be considered to be the cradle of the modern *Viverridae*, from where they radiated into the Ethiopian Region. They have never encroached upon the American territory (Scott, 1937). In the Quaternary the Oriental Region did not undergo such changes as the Holarctic did (lack of glaciations); in this connection it is characterized

by a huge diversity of environmental conditions of the tropical type, entailing a diversity of the fauna, in our case the carnivore one.

Fig. 58 shows clearly that the species inhabiting two basic biomes, tropical forests and savanna, are absolutely predominant. Especially many of the species living in tropical forests have evolved under these very conditions (about

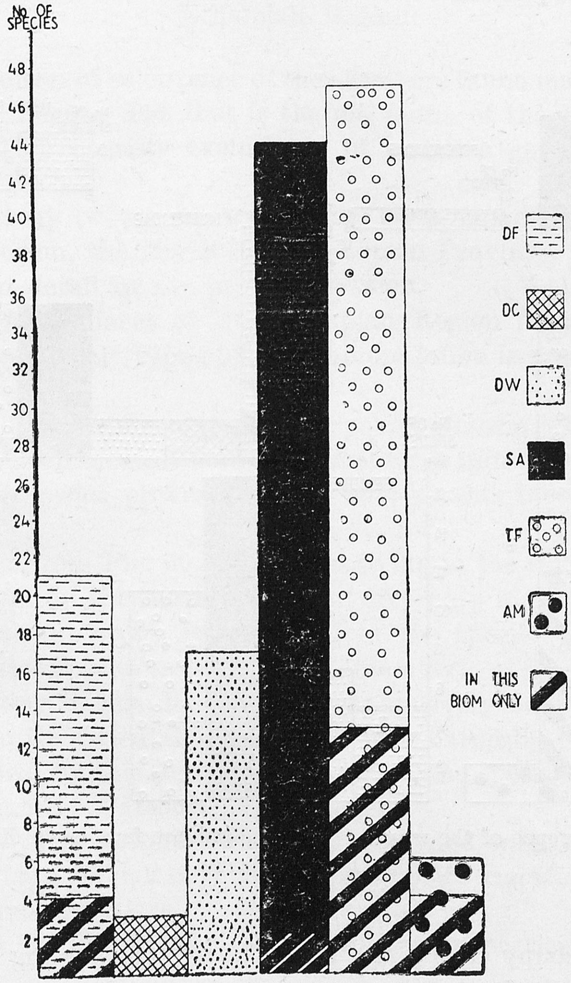


Fig. 58. The ecological type of the carnivore faunas of the Oriental Region

28 per cent of the total of species living in this biome). The corresponding value for the savannas is below 5 per cent. This is the presence of tropical forests that brings about the great diversity of species.

Deciduous forests are also of great importance. They occur on the boundary between the Oriental and Holarctic Regions, where the faunas of these regions come into contact (the Holarctic species do not generally go beyond this biome, the *Canidae* being an exception).

The next biome in which relatively many species occur is that of hot deserts, where, however, the exclusively desert species are wanting.

The distribution of the members of particular families in the biomes is illustrated by Fig. 59. This graph shows clear environmental preferences, especially those of the *Viverridae*, which have the most species (nearly 50 per cent) living nowhere but in tropical forests. Savanna is another biome important to this family.

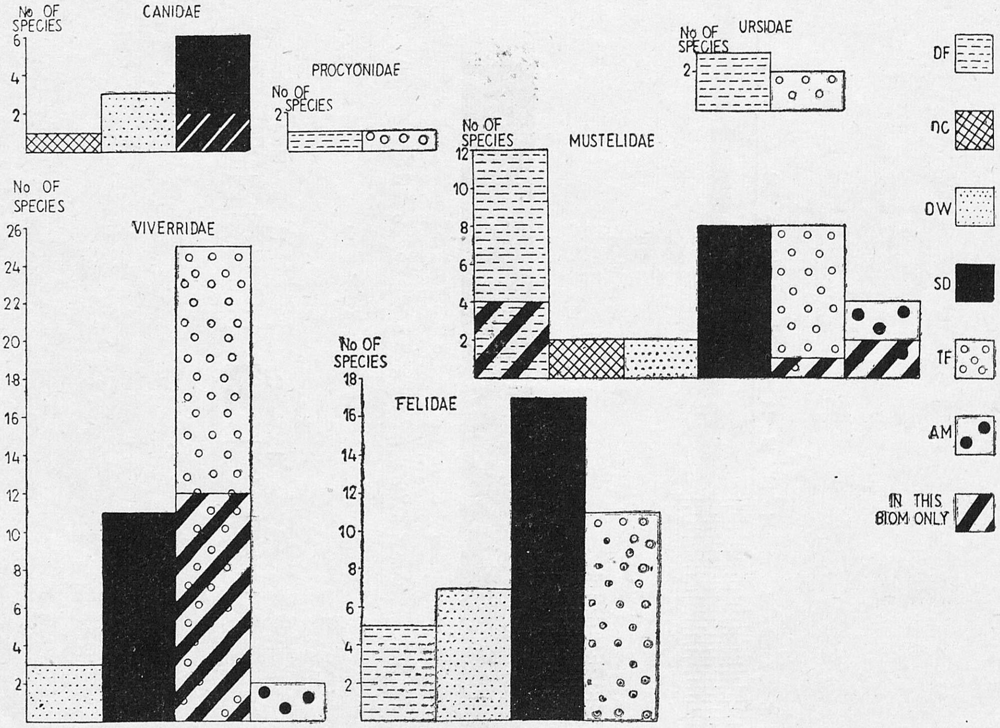


Fig. 59. The occurrence of the members of the carnivore families in different biomes of the Oriental Region

The *Felidae* occupy chiefly the biome of savannas, being less numerous in tropical forests and hot deserts.

As to the *Mustelidae*, the graph reveals the two-peak nature of their occurrence; the peaks are formed here by the biome of deciduous forests and that of tropical forests and savannas. One-third of the species of the deciduous forests are inhabitants of this biome only. Four species of the *Mustelidae* occur exclusively in amphibious environments.

The *Canidae* are encountered only in open areas, that is, in savannas and hot and cold deserts; they do not enter tropical forests. The situation is typical of this family, as these animals do not appear in tropical forests except in the Neotropical Region.

The Oriental species of the *Ursidae* (*Ursus malayanus* and *Ursus ursinus*) are present both in tropical and in deciduous forests and the Holarctic form, *Ursus thibetanus*, occurs in deciduous forests here.

The only species of the *Procyonidae*, *Ailurus fulgens*, is met with in deciduous forests, but it also occurs occasionally in tropical forests.

Ethiopian Region

Three main centres of occurrence of the carnivore fauna may be distinguished in the Ethiopian Region. The first is the old fauna of the Malagasy Province (Madagascar), which consists exclusively of endemic genera and species of the *Viverridae*.

The second group covers the transitional zone between the Holarctic and the Ethiopian Region, the North African-Yemen Province. This province has been discussed in detail in the previous section.

The remaining provinces of the Ethiopian Region form the third group in which the „viverroidal" type of the carnivore fauna is preserved in its original form.

The history of this fauna is relatively poorly known, which is due to the scantiness of palaeontological materials. The large number of well-specialized species of the *Viverridae* proves the long stay of this family in the African continent.

As will be seen from Fig. 60, the species living in the savanna are the most numerous and contain the most forms that live only in one biome.

Another important group is composed of the species of tropical forests; 25 per cent of these species inhabit this biome only.

The forms living in hot deserts are comparatively numerous (much more numerous than in the Oriental Region), which is naturally connected with the large areas occupied by this formation. However, the species living only in this biome are not numerous (below 10 per cent).

The relatively large number of species associated with water environment is an interesting fact, though only one species (*Lutra maculicauda*) lives exclusively in this environment.

Fig. 61 shows the distribution of the members of particular families in the biomes.

The family *Viverridae*, which is represented most numerously in this region, occurs chiefly in savannas and tropical forests. Here we are, therefore, concerned with the inversion of the situation found in the Oriental Region. It is merely natural, as these two regions have hardly two genera, *Genetta* and *Herpestes*, in common, and only the second of them is widely distributed in them. Nearly 50 per cent of the savanna species occur nowhere else but in them and about 35 per cent of the species of tropical forests only in this biome. The Oriental Region lacks exclusively savanna viverroid species and those occurring only in the tropical forest make about 50 per cent. This fact shows that the ecolo-

gical type of the Ethiopian *Viverridae* is quite different. No more than 6 species live in hot deserts and 2 of them nowhere else but in them.

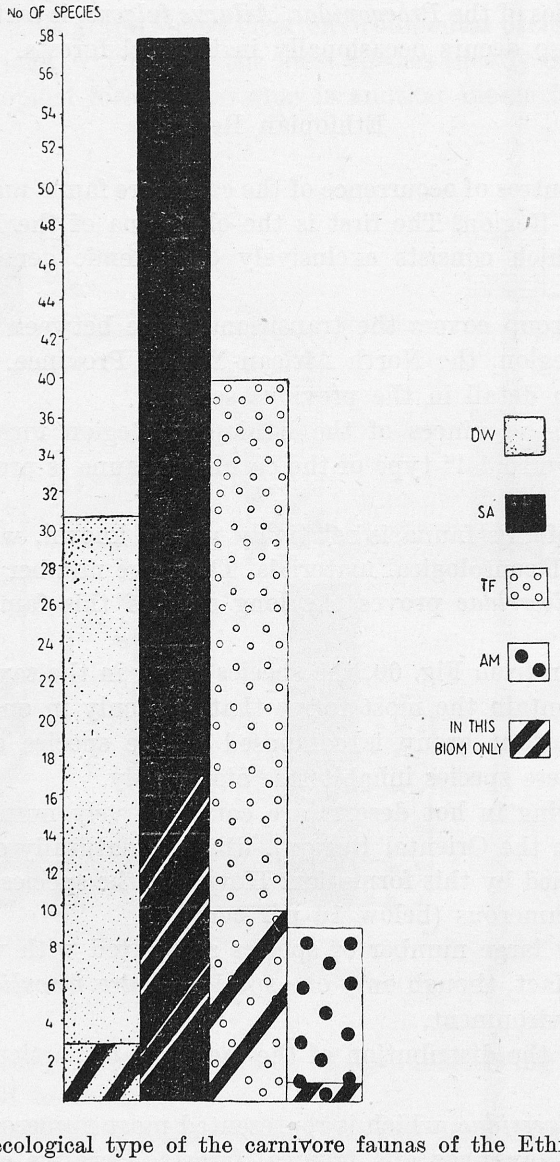


Fig. 60. The ecological type of the carnivore faunas of the Ethiopian Region

The *Mustelidae* are more or less uniformly distributed in all the biomes, that of tropical forests showing a slight predominance. Hardly 2 species are confined to only one biome, *Lutra maculicauda*, mentioned above, and *Mustela numidica*, which inhabits no other biomes but that of hot deserts.

The *Felidae* occur chiefly in the savanna and hot desert, hardly 3 species in tropical forests. There are no species specialized for life in one biome only.

The *Canidae* and *Hyaenidae* appear solely in hot deserts and savannas. 37·5 per cent of the savanna *Canidae* (3 species) live exclusively in this biome.

It may be assumed, in general, that in the Ethiopian carnivore fauna there are very few forms, except for the *Viverridae*, narrowly specialized for life in one biome, which indicates that this fauna is relatively young.

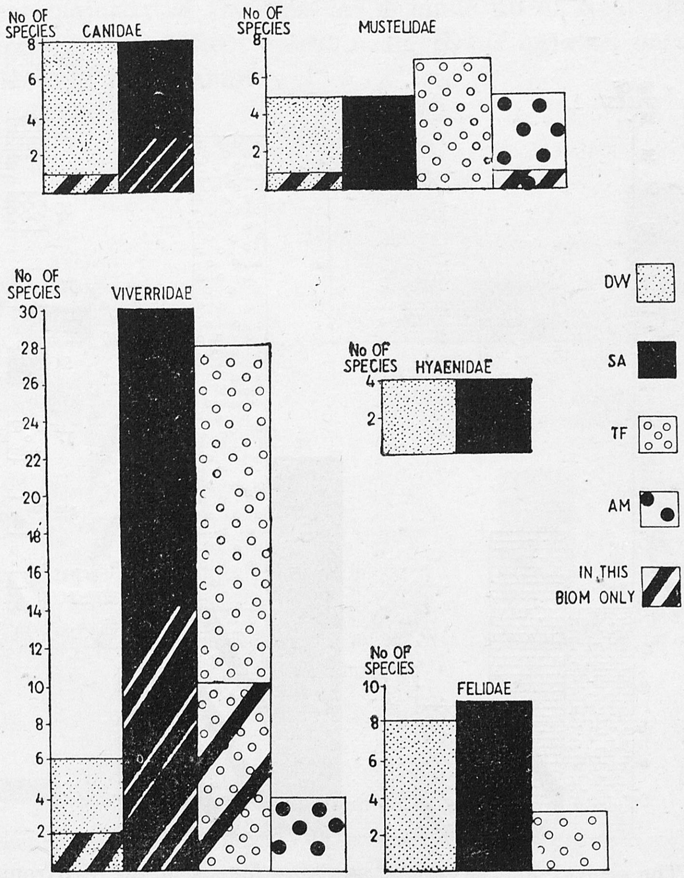


Fig. 61. The occurrence of the members of the carnivore families in different biomes of the Ethiopian Region

Neotropical Region

Some historical notes on the Neotropical fauna were given in the previous section. The *Carnivora* of this region are all of North American origin (Scott, 1937). The specific geobotanical and climatic conditions undoubtedly influenced the diversity of this fauna. This is evidenced, among other things, by the relatively large number of the species specialized for life in one biome only (Fig. 62).

The forms living in tropical forests, savannas and steppes are the most numerous. The large number of species associated with water environment has

probably been brought about by the excessive taxonomic division of the genus *Lutra*.

The relatively large number of species which occur in the biome of cold deserts (deserts in the Andes) is noteworthy. About 30 per cent of the species occurring in the biome of tropical forests do not appear outside this formation. In addition, over 30 per cent of the species are associated with the steppe only.

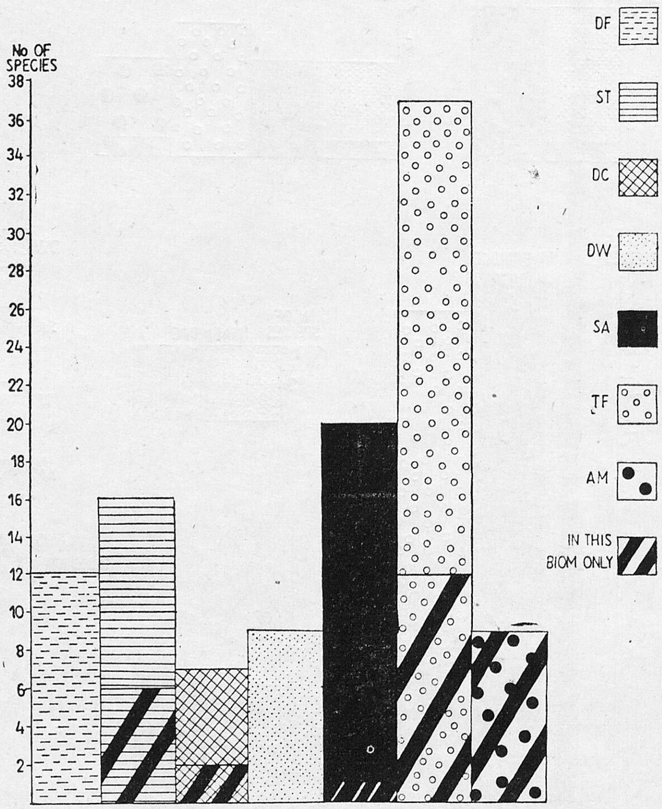


Fig. 62. The ecological type of the carnivore faunas of the Neotropical Region

Fig. 63 illustrates the occurrence of particular families in the biomes. The most numerous family *Mustelidae* is distributed in all the biomes, but chiefly in tropical forests. This situation is completely different from those observed in the faunas discussed above, and therefore it should be supposed that it is connected with the different generic composition of the *Mustelidae* of this region. A relatively large number of species are confined in occurrence to only one biome.

The now typically Neotropical family *Procyonidae* is practically limited to the biome of tropical forests.

Like the *Mustelidae*, the *Felidae* occur in all the environments, but in largest numbers in the biomes of the tropical zone, i. e., in the savanna, tropical forest

and hot deserts. They are also comparatively numerous in the biome of cold deserts, where the only species confined to one biome, *Felis guigna*, occurs.

The *Canidae* are most numerous in steppes and forests of the temperate zone and only few in savannas. Out of the 3 species met with in tropical forests, one form is endemic, *Atelocynus microtis*.

Fifty per cent of the steppe species do not occur anywhere else outside this biome. The clear majority of the *Canidae* is made up of Neotropical genera.

The only species of the Neotropical bear, *Ursus ornatus*, occurs both in deciduous forests and in savannas.

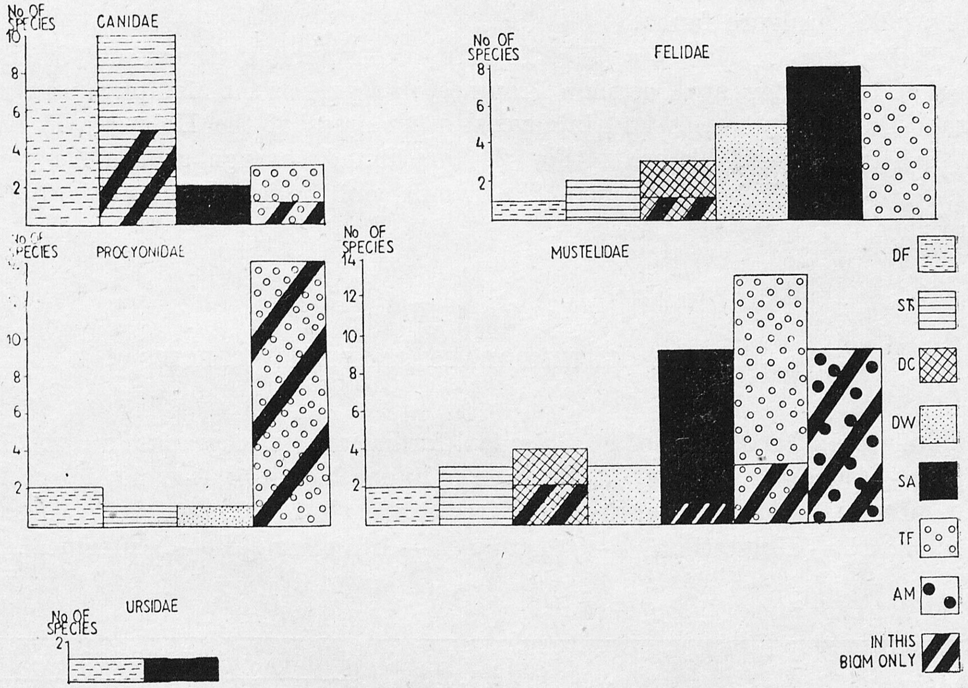


Fig. 63. The occurrence of the members of the carnivore families in different biomes of the Neotropical Region

C. Transitional Zones

It is quite obvious that between particular areas, provinces and regions there are more or less distinct transitional zones (Dechaseau, 1961), where the elements from the neighbouring territories mix together. The existence of such zones was emphasized in the discussions of particular provinces.

The exact demarcation of these territories is rather difficult, if possible at all. It will not be irrelevant to remind here of the well-known question of „Wallace's Line". A picture of the situation is given by Figs. 5, 16, 18 and 24, which show the range of occurrence of the elements of a given region in the remaining regions.

The Holarctic elements (Fig. 5) penetrate throughout the Oriental Region, nearly whole Neotropical Region, and the desert-savanna portion of the Ethiopian Region (as far as the equator). It must, however, be remembered that the share of Holarctic elements is, as a rule, low (below 10 per cent) and due to the occurrence of one or two species. The number of Holarctic species (and also that of elements from other regions) is larger only in borderlands.

The Oriental elements (Fig. 16) occur all over the Ethiopian Region and in nearly all the provinces of the Holarctic (except for the Boreal Province, where they appear only in a few areas). In the Ethiopian Region the Oriental elements are present throughout its area, but they form only a very low percentage of the whole carnivore fauna.

The Ethiopian elements (Fig. 18) are encountered in the whole Oriental Region, in the Levanto-Turanian Province, in a part of the Mediterranean and Arabo-Punjab Provinces and in several other areas of the Holarctic Region.

The Neotropical elements (Fig. 24) are found throughout the American Province of the Holarctic Region. The boundary of the formations of the Boreal Province is impassable for them.

V. A LIST OF CONTEMPORARY CARNIVORE SPECIES

Explanation: Denotation of geobotanical formations as in graphs (see p. 352.) STB — stenobiotic species, occurring in only one biome, E — endemic species. No. of units — number of working areal units in which the species occurs. Region: H — Holarctic, O — Oriental, E — Ethiopian, N — Neotropical.

Species	Geobotanical Formation	Occurrence			
		STB	E	No. of units	Region
Canis lupus LINNAEUS	TD, TG, DF, ST, ME, DC, DW, SA	—	—	55	H, O, E
Canis aureus LINNAEUS	ST, ME, SA, DW	—	—	28	E, O, H
Canis dingo MEYER	SA			1	Austr.
Canis latrans SAY	ST, DF, TG	—	—	16	H, N
Canis niger BARTRAM	ST	+	+	2	H
Canis adustus SUNDEVALL	SA, DW	—	—	8	E
Canis mesomelas SCHREBER	SA	+	—	4	E
Alopex lagopus LINNAEUS	TD, TG	—	—	9	H

Species	Geobotanical Formation	Occurrence STB	E	No. of units	Region
Vulpes vulpes LINNAEUS	TD, TG, DF, ST, ME, DC, DS, SA	—	—	55	H, O, E
Vulpes bengalensis SHAW	SA	+	—	4	O
Vulpes cana BLANFORD	SA	+	—	3	O
Vulpes corsac LINNAEUS	ST, DC	—	—	4	H
Vulpes ferrilata HODGSON	ST, DC	—	—	3	O
Vulpes chama THOMAS	SA	+	+	1	E
Vulpes rupelli SCHINTZ	DW, SA	+	—	10	E
Vulpes macrotis MERRIAM	ST	+	—	4	H
Vulpes velox SAY	ST	+	—	2	H
Vulpes pallida CRETZHMAR	DW, SA	—	—	3	E
Fennecus zerda ZIMMERMAN	DW	+	—	7	E, H
Urocyon cinereoargenteus SCHREBER	DF, ST	—	—	12	H, N
Urocyon littoralis BAIRD	DF, ST	—	+	1	H
Nyctereutes procyonoides GRAY	DF	—	—	4	H
Dusicyon australis KERR	ST	+	+	1	N
Dusicyon gracilis BURMEISTER	ST	+	—	1	N
Dusicyon fulvipes MARTIN	ST	+	—	1	N
Dusicyon inca THOMAS	ST, DF	—	—	1	N
Dusicyon culpaeus MOLINA	ST, DF	—	—	3	N
Dusicyon culpaeola THOMAS	ST	+	—	1	N
Dusicyon vetulus LUND	ST	+	—	3	N
Chrysocyon brachyurus ILLIGER	ST	+	—	7	N
Speothos venaticus LUND	TF, SA	—	—	7	N
Cuon alpinus PALLAS	DF, SA	—	—	16	O, H
Atelocynus microtis SCLATER	TF	+	+	1	N
Cerdocyon thous LINNAEUS	SA, DF, TF	—	—	10	N
Lycaon pictus TEMMINCK	SA	+	—	12	E
Otocyon megalotis DESMAREST	DW	+	—	3	E
Ursus ornatus CUVIER	DF, SA	—	+	1	N
Ursus thibetanus CUVIER	DF, TG	—	—	9	H, O
Ursus arctos LINNAEUS	DF, TG	—	—	28	H
Ursus americanus PALLAS	DF, TG	—	—	13	H
Ursus maritimus PHIPPS	TD, AM	+	—	5	H
Ursus malayanus RAFFLES	TF, DF	—	—	3	O

Species	Geobotanical Formation	Occurrence			
		STB	E	No. of units	Region
Ursus ursinus SHAW	TF, DF	—	—	6	O
Bassariscus astutus LICHTENSTEIN	DF, ST, DW	—	—	7	H, N
Jentinkia sumichrasti SAUSSURE	TF	+	—	2	N
Procyon lotor LINNAEUS	DF	+	—	9	H, N
Procyon cancrivorus GOLDMAN	TF	+	—	9	H
Procyon insularis MERRIAM	TF	+	+	1	N
Procyon maynardii BANGS	TF	+	+	1	N
Procyon pygmaeus MERRIAM	TF	+	+	1	N
Procyon minor MILLER	TF	+	+	1	N
Procyon gloveralleni NELSON and GOLDMAN	TF	+	+	1	N
Nasua narica LINNAEUS	TF	+	—	5	N, H
Nasua nasua LINNAEUS	TF	+	—	8	N
Nasua nelsoni MERRIAM	TF	+	+	1	N
Nasuella olivacea GRAY	TF	+	+	2	N
Potos flavus G. ST. HILAIRE and G. CUVIER	TF	+	—	9	N
Bassaricyon gabbi ALLEN	TF	+	—	5	N
Bassaricyon pauli ENDERS	TF	+	—	5	N
Ailurus fulgens F. CUVIER	DF	+	—	3	O, H
Ailuropoda melanoleuca DAVID	DF	+	+	2	O
Mustela erminea LINNAEUS	TD, TG, DF, ST, ME, DC, DW, SA	—	—	34	H, O, E
Mustela nivalis LINNAEUS	TD, TG, DF, ST, ME, DC, DW	—	—	38	H, O, E
Mustela altaica PALLAS	TG, DF, ST	—	—	9	H, O
Mustela kathiah HODGSON	DF, ST	—	—	6	H, O
Mustela sibirica PALLAS	TG, DF, ST	—	—	14	H, O
Mustela lutreola LINNAEUS	TG, DF	—	—	4	H
Mustela strigidorsa GRAY	DF	+	+	1	O
Mustela putorius LINNAEUS	TG, DF, ST, TD	—	—	18	H, O

Species	Geobotanical Formation	Occurrence			
		STB	E	No. of units	Region
Mustela rixosa BANGA	DF, ST	—	—	4	H
Mustela frenata LICHTENSTEIN	TF, SA	—	—	31	N, H
Mustela nigripes AUDUBON and BACHMAN	DF, ST	—	—	4	H
Mustela vison SCHREBER	TG, DF	—	—	11	H
Mustela paraense ALLEN	TF, SA	—	+	1	N
Mustela africans DESMAREST	TF, SA	—	—	6	N
Mustela numidica PUCHERAN	DW	+	+	1	E
Vormela peregusna GULDENSTAEDT	ST	+	—	11	H
Martes martes LINNAEUS	TG, DF	—	—	13	H
Martes foina ERXLEBEN	TG, DF	—	—	27	H
Martes melampus WAGNER	DF	+	—	2	H
Martes zibellina LINNAEUS	TG, DF	—	—	10	H
Martes flavigula BODDAERT	DF	+	—	10	H, O
Martes gwatkinsi HORSFIELD	DF	+	+	1	O
Martes americana TURTON	DF, ST	—	—	4	H
Martes pennanti ERXLEBEN	DF, ST	—	—	5	H
Tayra barbara HAMILTON-SMITH	TF	+	—	11	N
Grison vittatus SCHREBER	SA, TF	—	—	12	N
Grison cuja BELL	SA, TF	—	—	12	N
Lyncodon patagonicus BLAINVILLE	SA	+	+	1	N
Ictonyx striatus PERRY	SA, TF	—	—	10	E
Poecilictis libyca HEMPRICH and EHRENBERG	SA, DW	—	—	4	E
Poecilogale albinucha GRAY	SA, TF, DW	—	—	5	E
Gulo gulo LINNAEUS	TG, TD	—	—	17	H
Mellivora capensis SCHREBER	TF, SA, ST	—	—	17	E, H, O
Meles meles LINNAEUS	TG, DF	—	—	29	H
Arctonyx collaris F. CUVIER	DF, ST, TF	—	—	7	O, H
Mydaus javanensis F. CUVIER	TF	+	+	1	O
Suillotaxus marchei LAWRENCE	TF, SA	—	+	1	O
Taxidea taxus SCHREBER	ST	+	—	8	H
Melogale personata GEOFFROY	DF, TF, SA	—	—	3	O
Melogale moschata GRAY	DF, TF, SA	—	—	5	O, H
Melogale orientalis GRAY	DF, TF, SA	—	+	1	O

Species	Geobotanical Formation	Occurrence			
		STB	E	No. of units	Region
Mephitis mephitis E. G. St. Hilaire and G. Cuvier	DF, ST, DC	—	—	6	H
Mephitis macroura Lichtenstein	DF, ST, DW	—	—	3	H, N
Spilogale putorius Gray	DF, ST, DC, DW	—	—	10	H, N
Spilogale pygmea Thomas	TF, DW	—	+	1	N
Conepatus mesoleucus Lichtenstein	ST, TF	—	—	4	N, H
Conepatus semistriatus Gmelin	TF	+	+	1	N
Conepatus rex Thomas	DC	+	+	1	N
Conepatus humboldti Gray	DC	+	+	1	N
Conepatus suffocans Illiger	SA, TF	—	—	7	N
Conepatus castaneus D'Orbigny and Gervais	ST	+	+	1	N
Conepatus chinga Molina	SA, TF	—	—	4	N
Conepatus amazonicus Lichtenstein	SA, TF	—	—	3	N
Conepatus quitensis Humbolt	TF	+	+	1	N
Lutra incarum Thomas	AM	+	—	2	N
Lutra platensis Waterhouse	AM	+	—	5	N
Lutra enudris Fisher	AM	+	—	2	N
Lutra felina Molina	AM	+	—	2	N
Lutra provocax Thomas	AM	+	—	2	N
Lutra mitis Thomas	AM	+	—	3	N
Lutra annectens Major	AM	+	—	2	N
Lutra colombiana Allen	AM	+	+	1	N
Lutra lutra Linnaeus	AM	+	—	44	H, O
Lutra canadensis Schreber	AM	+	—	11	H
Lutra maculicauda Lichtenstein	AM	+	—	7	E
Lutra sumatrana Gray	AM	+	—	2	O
Lutrogale perspicillata Geoffroy	AM	+	—	5	O
Pteronura brasiliensis Gmelin	AM	+	—	6	N
Amblyonyx cinerea Illiger	AM	+	—	8	O
Aonyx capensis Schintz	SA, TF, AM	—	—	6	E

Species	Geobotanical Formation	Occurrence			
		STB	E	No. of units	Region
Paraonyx microdon POHLE	TF, AM	—	+	1	E
Paraonyx congica LONNBERG	TF, AM	+	—	3	E
Paraonyx philippai HINTON	TF, AM	—	+	1	E
Enhydra lutris LINNAEUS	AM	+	+	2	H
Poiana richardsoni THOMPSON	TF	+	—	2	E
Genetta genetta LINNAEUS	TF, SA, ME, DF	—	—	15	E, H
Genetta maculata GRAY	TF, SA	—	—	2	E
Genetta lehmanni KUHN	TF	+	+	1	E
Genetta servalina PUCHERAN	TF, SA	—	—	4	E
Genetta tigrina SCHREBER	TF, SA	—	—	11	E
Viverricula indica DESMAREST	TF	+	—	10	O
Osbornictis piscivora ALLEN	TF, AM	+	+	1	E
Viverra megaspila BLYTH	TF, SA	—	—	4	O
Viverra zibetha LINNAEUS	TF, SA	—	—	6	O
Viverra tangalunga GRAY	TF, SA	+	+	1	O
Civettictis civetta SCHREBER	SA	+	—	4	E
Prionodon linsang HARDWICKE	TF	+	+	1	O
Prionodon pardicolor HODGSON	TF	+	—	3	O
Nandinia binotata GRAY	TF	+	—	4	E
Arctogalidia trivirgata GRAY	TF	+	—	4	O
Paradoxurus hermaphroditus PALLAS	TF	+	—	11	O
Paradoxurus zeylonensis PALLAS	TF	+	+	2	O
Paradoxurus jerdoni BLANFORD	TF	+	—	2	O
Paguma larvata HAMILTON-SMITH	TF, SA	—	—	9	O, H
Macrogalidia musschenbroecki SCHWARTZ	TF	+	+	1	O
Arctictis binturong RAFFLES	TF	+	—	5	O
Fossa fossa SCHREBER	SA	+	+	1	E
Hemigalus derbyanus GRAY	TF	+	+	1	O
Chrotogale owstoni THOMAS	TF	+	+	1	O
Diplogale hosei THOMAS	TF	+	+	1	O
Cynogale bennetti GRAY	TF, AM	—	—	2	O
Eupleres goudotti DOYERE	TF, SA	—	+	3	E
Eupleres major LAVAUDEN	TF, SA	—	+	3	E

Species	Geobotanical Formation	Occurrence			
		STB	E	No. of units	Region
Galidia elegans I. GEOFFROY	TF	+	+	3	E
Galidictis striata I. GEOFFROY	TF	+	+	1	E
Galidictis fasciata GMELIN	TF	+	+	1	E
Mungotictis lineatus POCOCK	TF	+	+	3	E
Mungotictis substriatus POCOCK	TF	+	+	3	E
Salancia unicolor GRAY	?	?	+	3	E
Salancia olivacea GRAY	?	?	+	3	E
Suricata suricatta SCHREBER	SA	+	—	3	E
Herpestes ichneumon LINNAEUS	TF, SA, ME	—	—	11	O, E, H
Herpestes javanicus GEOFFROY	TF, SA	—	—	2	O
Herpestes auropunctatus HODGSON	TF, SA, DW	—	—	10	O
Herpestes edwardsi GEOFFROY	TF, SA, DW	—	—	12	O
Herpestes smithi GRAY	DW, SA	—	—	6	O, H
Herpestes fuscus WATERHOUSE	TF, SA, DW	—	—	4	O
Herpestes vitticollis BENNETT	TF, SA	—	—	4	O
Herpestes urva HODGSON	TF, SA	—	—	4	O
Herpestes ochracea GRAY	TF, SA	—	—	3	E
Herpestes cauui SMITH	TF, SA	—	—	5	E
Herpestes dentifer HELLER	SA	+	+	1	E
Herpestes granti GRAY	SA	+	+	1	E
Herpestes ignitus ROBERTS	SA	+	+	1	E
Herpestes nigratus THOMAS	DW	+	+	1	E
Herpestes pulverulentus WAGNER	SA, DW	—	—	2	E
Herpestes ratlamuchi SMITH	SA	+	—	2	E
Herpestes ruddi THOMAS	DW	+	+	1	E
Herpestes sanguineus RUPELLI	DW, TF, SA	—	—	7	E
Helogale parvula SUNDEVALL	SA, TF	—	—	7	E
Dologale dybowskii POUSARGUES	?	?	—	2	E
Atilax paludinosus G. CUVIER	TF, AM	—	—	8	E
Mungos mungo GMELIN	TF, AM	—	—	11	E
Crossarchus obscurus F. CUVIER	SA	+	—	4	E
Liberiictis kuhni HAYMAN	TF	+	+	1	E

Species	Geobotanical Formation	Occurrence			
		STB	E	No. of units	Region
Ichneumia albicauda G. CUVIER	TF, SA, AM	—	—	8	E
Bdeogale crassicauda PETERS	SA	+	—	2	E
Bdeogale tenuis THOMAS and WROUGHTON	SA	+	+	1	E
Bdeogale nigripes PUCHERAN	SA	+	—	2	E
Bdeogale jacksoni THOMAS	SA	+	+	1	E
Rhynchogale melleri GRAY	SA	+	—	2	E
Cynictis penicillata G. CUVIER	DW, SA	—	—	5	E
Paracynictis seloussi DE WINTON	SA	+	—	3	E
Cryptoprocta ferox BENNETT	TF, SA	—	+	3	E
Xenogale microdon ALLEN	TF	+	+	1	E
Proteles cristatus SPARRMAN	DW, SA	—	—	5	E
Crocuta crocuta ERXLEBEN	DW, SA	—	—	11	E
Hyaena hyaena LINNAEUS	SA, DW	—	—	15	E, H
Hyaena brunnea THUNBERG	DW, SA	—	—	2	E
Felis silvestris SCHREBER	DF, ME	—	—	11	H
Felis libyca FORSTER	DW, SA, ST	—	—	25	E, H, O
Felis bieti MILNE-EDWARDS	ST, SA, DW	—	—	3	O, H
Felis chaus GULDENSTAEDT	ST, SA, TF, DW	—	—	21	O
Felis margarita LOCHE	DW, SA, ST	—	—	4	E, O
Felis manul PALLAS	ST, DC	—	—	10	H
Felis serval SCHREBER	DW, SA, TF	—	—	11	E
Felis marmorata MARTIN	SA, TF	—	—	5	O
Felis temmincki VIGORS and HORSFIELD	DF, SA	—	—	5	O
Felis bengalensis KERR	SA, DF, TF	—	—	13	O, H
Felis planiceps VIGORS and HORSFIELD	TF, SA	—	—	2	O
Felis minuta TEMMINCK	TF, SA	—	+	1	O
Felis rubiginosa GEOFFROY	TF, SA	—	—	4	O
Felis viverrina BENNETT	TE, SA	—	—	7	O
Felis badia TEMMINCK	TF, SA	—	+	1	O
Felis nigripes BURCHELL	DW, SA	—	—	2	E
Felis concolor LINNAEUS	DC, DW, ST, SA, DF, TF, TG	—	—	19	H, N

Species	Geobotanical Formation	Occurrence			
		STB	E	No. of units	Region
Felis pardalis Linnaeus	TF, SA, DW	—	—	14	N, H
Felis wiedi Schintz	TF, SA, DW	—	—	9	N, H
Felis tigrina Erxleben	TF, SA	—	—	10	N
Felis yaguarundi Fischer	TF, SA, DW	—	—	14	N, H
Felis colocolo Molina	DW, SA, ST	—	—	9	N
Felis jacobita Cornalia	DC, ST	—	—	4	N
Felis geoffroyi D'Orbigny and Gervais	ST, SA	—	—	6	N
Felis guigna Molina	DC	+	+	2	N
Felis aurata Temminck	SA, TF	—	—	2	E
Lynx lynx Linnaeus	TG, DF	—	—	25	H
Lynx caracal Schreber	DW, ST	—	—	19	H, E, O
Lynx rufus Schreber	DW, ST	—	—	12	H, N
Panthera leo Linnaeus	SA, DW	—	—	13	E, O
Panthera pardus Linnaeus	DW, SA, TF, DF	—	—	33	E, O, H
Panthera onca Linnaeus	TF, SA	—	—	10	N, H
Panthera tigris Linnaeus	SA, TF, DF	—	—	15	O, H
Panthera nebulosa Griffith	TF, SA	—	—	7	O
Panthera uncia Schreber	DF, ST	—	—	5	H, O
Acinonyx jubatus Schreber	DW, SA	—	—	19	O, E, H

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STRESZCZENIE

Celem niniejszej pracy była próba zastosowania w zoogeografii ssaków metod statystycznych — diagramu CZEKANOWSKIEGO i dendrytowej. Metody diagramu CZEKANOWSKIEGO użył po raz pierwszy w zoogeografii KOSTROWICKI (1965) w swej pracy dotyczącej regionalizacji Palearktyki w oparciu o rozmieszczenie przedstawicieli rzędu *Lepidoptera (Insecta)*. Metoda dendrytowa nie była dotychczas stosowana w zoogeografii. Obie te metody są wysoce obiektywne i dają cenny materiał do interpretacji.

Wybrany do analizy statystycznej rząd *Carnivora (Mammalia)* jest dość liczny (247 gatunków), mniej więcej równomiernie rozsiedlony na różnych

kontynentach (z wyjątkiem Australii). Gatunki są wystarczająco dobrze poznane oraz zbadane są ich zasięgi występowania. Stanowisko systematyczne przeważającej liczby gatunków jest dobrze znane, wyjątkiem są niektóre dyskusyjne gatunki, które zostały omówione w rozdziale III.

Terytoria wszystkich kontynentów zostały podzielone na 113 roboczych jednostek przestrzennych (Australia została potraktowana jako jedna jednostka), opartych na formacjach geobotanicznych. Fauny *Carnivora* występujące w tych jednostkach zostały poddane analizie statystycznej, w wyniku której niektóre jednostki zostały połączone w większe jednostki. Stanowi to oryginalny wynik pracy. Lista tych jednostek — regionów zoogeograficznych — przedstawiona jest w rozdziale III.

Poszczególne krainy zoogeograficzne zostały podzielone na prowincje i regiony. Fauna każdej prowincji przedstawiona jest na wykresie, obrazującym procentowy skład rodzin *Carnivora* w danej faunie oraz liczbę gatunków w każdej rodzinie.

Z wykresów tych wynika, iż typową fauną *Carnivora* dla Krainy Etiopskiej i Orientalnej jest fauna typu „viverroidalnego" — z przewagą przedstawicieli *Viverridae*, a dla pozostałych krain typu „musteloidalnego" — z przewagą przedstawicieli *Mustelidae*.

W wykresach tych uwzględniono również procent elementów obcych, pochodzących z innych krain, w danej faunie. Pokazuje to stopień penetrowania badanej prowincji przez te elementy, jak również umożliwia wykazanie gatunków najbardziej aktywnych w penetracji — są to najczęściej przedstawiciele *Felidae*.

W wyniku analizy statystycznej Afryka Północna, zazwyczaj zaliczana do Krainy Holarktycznej, została włączona do Krainy Etiopskiej. Region ten wykazuje najwyższe pokrewieństwa do pozostałych regionów Krainy Etiopskiej, posiadając jednak wyraźnie przejściowy charakter.

W rozdziale IV zostało omówione m. in. występowanie rodzin *Carnivora*. Przy poszczególnych rodzinach analizowano występowanie jej przedstawicieli w różnych biomach, liczbę roboczych jednostek przestrzennych objętych występowaniem danego gatunku, oraz strukturę areograficzną w biomach. Analizowano również historię danej rodziny.

Rodzina *Canidae* — typowym środowiskiem są przestrzenie bezleśne, gatunki o niezbyt dużych areałach. Formy o małych areałach spotykane głównie na stepach i sawannach. Tylko trzy gatunki występują w lasach tropikalnych.

Rodzina *Ursidae* — gatunki związane ze środowiskiem leśnym (wyjątkami są *Ursus maritimus* — forma arktyczna i *U. ornatus* występujący również w sawannie). Małe areały, wyjątkiem jest tylko *U. arctos*.

Rodzina *Procyonidae* — w chwili obecnej typowo neotropikalna, stanowiska w Azji mają charakter reliktowy. Większość gatunków to mieszkańcy biomu lasu tropikalnego, formy holarktyczne występują w lasach liściastych. *Procyonidae* mają na ogół małe zasięgi, są raczej stenobiotyczne.

Rodzina *Mustelidae* — najliczniejsza wśród *Carnivora*. Jej przedstawiciele występują we wszystkich biomach, dużo form ziemnowodnych. Rodzina zdecy-

dowanie eurybiotyczna, co świadczy o dużej jej plastyczności. Gatunki holarktyczne mają największe zasięgi występowania — np. *Mustela erminea*, *M. nivalis*, *Lutra lutra*. Wśród form holarktycznych prawie nie ma gatunków wyspecjalizowanych do życia w jednym biomie. Świadczy to m. in. o stosunkowo niedawnym zasiedleniu Holarktyki przez *Mustelidae* (w przeciwieństwie do gatunków paleotropikalnych z tej rodziny).

Rodzina *Viverridae* — druga pod względem liczebności wśród *Carnivora*, stara, wyraźnie paleotropikalna. Przedstawiciele jej głównie występują w sawannach i lasach tropikalnych, z tym że etiopskie *Viverridae* przede wszystkim w sawannie, a orientalne w lasach tropikalnych. Stosunkowo licznie spotykane w biomie pustyń gorących. Niezbyt duże zasięgi występowania, stosunkowo dużo gatunków żyje tylko w jednej roboczej jednostce przestrzennej. Wydaje się, że taksonomia niektórych rodzajów (*Genetta*, *Herpestes*) jest zbyt rozbudowana, prawdopodobnie niektóre formy podawane jako gatunki są tylko podgatunkami.

Rodzina *Hyaenidae* — obecnie ograniczona do biomów sawanny i pustyń Krainy Etiopskiej i Holarktycznej.

Rodzina *Felidae* — wyraźnie związana ze strefą gorącą. Brak wąskiej specjalizacji do życia w jednym biomie. Gatunki z tej rodziny mają na ogół duże zasięgi występowania. Stosunkowo mniejsze zasięgi mają formy neotropikalne.

Na rycinach 57—64 podane zostały informacje dotyczące ekologicznych typów fauny *Carnivora* objętych całościowo (odnośnie do krain, jak i w rozbiciu na poszczególne rodziny). Wynika z nich przede wszystkim względna młodość faun Krainy Holarktycznej w przeciwieństwie do wyraźnie starszych faun paleotropikalnych i neotropikalnych. Związane to jest z występowaniem zlodowaceń na terenie Holarktyki. W tej części pracy zostały również przeanalizowane dzieje faun *Carnivora* w poszczególnych krainach.

Poddano analizie występowanie elementów z poszczególnych krain penetrujących krainy ościenne (rozdział IV).

W rozdziale V podana jest lista współcześnie żyjących gatunków *Carnivora*, z uwzględnieniem biomu, w którym one występują, charakteru występowania (formy stenobiotyczne i endemity) oraz liczby roboczych jednostek przestrzennych objętych występowaniem danego gatunku.

РЕЗЮМЕ

Настоящее исследование представляет собою опыт применения в зоогеографии млекопитающих статистических методов — диаграмм Чекановского и дендритовой. Метод диаграммы Чекановского впервые был использован в зоогеографии Костровицким (Kostrowicki, 1965) с целью регионализации Палеарктики на основании особенностей географического распространения представителей отряда чешуекрылых насекомых. Метод дендритов до настоящего времени не находил применения в подобного рода исследованиях. Оба метода достаточно

объективны и доставляют весьма ценный материал для интерпретации и обобщений.

Избранный для статистического анализа отряд хищных млекопитающих имеет достаточно большой объем — 247 видов, более или менее равномерно распространенных по всем континентам (за исключением Австралии). Изученность видов отряда, в том числе и их ареалов, вполне удовлетворительна. Систематическое положение подавляющего числа видов выяснено хорошо, за исключением лишь нескольких спорных видов, обсуждаемых в разделе III настоящей работы.

Территории всех континентов были разделены на 113 пространственных рабочих подразделений (Австралия представляет собой одно из таких подразделений), на основании геоботанических данных. Фауны хищных, представленные в этих подразделениях, были подвергнуты статистической обработке, в результате которой некоторые подразделения были объединены в подразделения более высокого порядка. Эти сведения представляют собой оригинальный результат настоящей работы. Список этих подразделений — зоогеографических регионов приводится в разделе III.

Отдельные зоогеографические области были разделены на провинции и регионы. Фауна каждой провинции представлена на графике, отражающем процентный состав семейств хищников в данной фауне и количество видов в каждом семействе.

Из этих графиков видно, что, например, фауна Эфиопской и Ориентальной областей относится к „виверроидному“ типу по причине преобладания здесь представителей *Viverridae*, а остальных областей — к „мустелоидному“, т. к. здесь численным преимуществом обладают представители *Mustelidae*.

В этих графиках учтен также процент чужеродных элементов фауны данного подразделения, которые происходят из других областей. Этот показатель дает возможность судить о степени проникновения чужеродных элементов в фауну данной провинции, а также установить виды, отличающиеся наибольшей склонностью к проникновению в другие провинции из мест своего обычного распространения; чаще всего таковыми являются представители *Felidae*.

Использование статистического метода привело к тому, что Северную Африку, обычно относимую к Голарктической области, следовало бы отнести к Эфиопской. Этот регион, хотя и характеризуется огромной степенью сродства со многими регионами Эфиопской области, отличается хорошо выраженным переходынм (эфиопско-голарктическим) характером.

В разделе IV обсуждаются вопросы географического распространения семейств хищных. Для каждого семейства приводится анализ представительства его видов в различных биомах, количество рабочих пространственных подразделений, обнимаемых ареалом каждого вида, и ареографическая структура в биомах. Обсуждается также история каждого семейства.

Семейство *Canidae*. Типичная среда — безлесные пространства; видовые ареалы невелики. Формы, имеющие малые ареалы, встречаются главным образом в степях и саваннах. Лишь три вида встречаются в тропических лесах.

Семейство *Ursidae*. Виды, связанные с лесами (исключениями являются

Ursus maritimus — арктическая форма, и *U. ornatus*, встречающийся также в саванне). Ареалы малы, за исключением *U. arctos*.

Семейство *Procyonidae*. В настоящее время типично неотропическое семейство, местонахождения в Азии имеют реликтовый характер. Большинство видов являются обитателями биома тропического леса, голарктические формы встречаются в лиственных лесах. Ареалы невелики; виды по большей части стенобионтны.

Семейство *Mustelidae*. Наиболее многочисленное семейство в отряде. Его представители встречаются во всех биомах; много земноводных форм. Семейство отличается хорошо выраженной эврибионтностью, что свидетельствует о значительной его пластичности. Голарктические виды отличаются крупным размером ареалов *(Mustela erminea, M. nivalis, Lutra lutra)*. Среди голарктических форм практически отсутствуют виды, приспособленные к жизни только в одном биоме. Это, между прочим, должно свидетельствовать о недавнем заселении Голактики представителями семейства (в противоположность палеотропическим представителям семейства).

Семейство *Viverridae*. Второе по численности видов семейство в отряде хищных. Связано с палеотропиками. Виды чаще всего встречаются в саванее и тропических лесах, причем эфиопские *Viverridae* предпочитают саванну, а ориентальные — тропические леса. В сравнительно большом числе встречаются в биоме жарких пустынь. Ареалы не очень велики. Имеется значительное число видов, ареал которых не выходит за пределы одного рабочего пространственного подразделения. Весьма вероятно, что систематика некоторых родов *(Genetta, Herpestes)* слишком загромождена, и некоторые формы, принимаемые за виды, являются в самом деле лишь подвидами.

Семейство *Hyaenidae*. В настоящее время распространение ограничено биомами саванны и пустынь Эфиопской и Голарктической областей.

Семейство *Felidae*. Тесно связано с жарким поясом. Отсутствие узкой специализации к жизни в одном биоме. Виды семейства, как правило, отличаются весьма обширными ареалами. Значительно меньшие ареалы имеют неотропические формы.

Графики фиг. 57—64 отражают данные об экологических типах фаун хищных, как в целом (в объеме областей), так и для отдельных семейств. Приведенные на них данные показывают относительную молодость фауны Голарктики в противоположность более древним палеотропическим и неотропическим фаунам. Это связывается с существованием оледенений на территории Голарктики. В этой же части работы приводится анализ истории фаун хищных в отдельных областях.

Анализируется также наличие элементов соседних областей, проникших в данную область (раздел IV).

Раздел V содержит список современных видов *Carnivora* с учетом биома, в котором они встречаются, характера распространения (стенобионтные формы и эндемики), а также список рабочих пространственных подразделений, перекрытых ареалом данного вида.

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